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(BIOLOGIA VEGETAL)

FENOLOGIA DA DISPERSÃO E ESTRATÉGIAS DE GERMINAÇÃO DE SEMENTES DE PLANTAS LENHOSAS E HERBÁCEAS NO CERRADO

DIEGO FERNANDO ESCOBAR ESCOBAR

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ciencias biológica, ênfase em biologia vegetal.

Agosto – 2019

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TÍTULO DA TESE: FENOLOGIA DA DISPERSÃO E ESTRATÉGIAS DE GERMINAÇÃO DE SEMENTES DE PLANTAS LENHOSAS E HERBÁCEAS NO CERRADO

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RESUMO

A germinação de sementes e estabelecimento de plântulas são as etapas iniciais e cruciais do ciclo de vida das plantas, sendo importantes determinantes dos padrões de distribuição, diversidade e dinâmica das comunidades vegetais. Nos ecossistemas sazonais, a disponibilidade de água no solo e a heterogeneidade do ambiente são os principais fatores limitantes da germinação e estabelecimento das plântulas. Nestes ambientes a fenologia da dispersão das sementes, o nicho de germinação e a dormência devem sincronizar a germinação com o início da estação chuvosa, o que maximiza o período favorável ao estabelecimento, incrementando as chances de sobrevivência das plântulas à subsequente estação seca. Por outro lado, as plantas respondem à heterogeneidade ambiental distribuindo a progênie através do espaço ou do tempo. Distribuir as sementes ao longo de diferentes áreas aumenta a chance de que pelo menos uma parte delas chegue a lugares adequados para a germinação e estabelecimento das plântulas. Por outro lado, a dormência incrementa a variação do tempo de germinação distribuindo a germinação em vários eventos, o que diminui a probabilidade de que todas as plântulas morram devido a eventos imprevisíveis. Os estudos dos mecanismos que sincronizam a germinação com o início da estação chuvosa nos ambientes tropicais sazonais não levam em consideração o nicho de germinação nem a história evolutiva das espécies, e estão focados majoritariamente nos ecossistemas florestais. Portanto, não temos uma clara compreensão da importância relativa e da interação dos diferentes mecanismos que controlam o tempo de germinação nos ambientes sazonais tropicais, nem de como são afetados por outras características da história natural e evolutiva das espécies. Além disso, o papel da dormência (i.e., dispersão temporal) como mecanismo para enfrentar a heterogeneidade ambiental tem sido pouco explorado nos ambientes sazonais. Desta forma, nesta tese avaliei os mecanismos que as plantas do cerrado utilizam para sincronizar a germinação com o início da estação chuvosa, e para enfrentar a heterogeneidade ambiental, e como variam tais mecanismos em relação a características funcionais e evolutivas das espécies. Para tanto, caracterizei o nicho térmico de germinação e a dormência mediante experimentos de germinação, e a síndrome de dispersão, a fenologia da dispersão, o peso das sementes e a forma de crescimento de 82 espécies de cerrado de 26 famílias, que incluem as principais linhagens de angiospermas e uma ampla gama de formas de crescimento. Os resultados mostram que a dormência é uma característica adaptativa no cerrado, já que incrementa as chances de estabelecimento das plântulas ao sincronizar a germinação com o início da estação chuvosa e distribuir o risco de recrutamento das espécies com capacidade limitada de dispersão espacial (i.e., autocóricas). A dormência está correlacionada evolutivamente com a dispersão espacial, mas não com o peso das sementes ou a fenologia da dispersão, indicando um *trade-off* entre a dispersão espacial e temporal. Além disso, a dormência e o nicho de germinação são mecanismos alternativos para enfrentar a sazonalidade climática e a importância relativa destes mecanismos varia com a estação de dispersão. Desta forma, a dormência é chave para entender a grande diversidade vegetal do cerrado, não só porque incrementa as chances de estabelecimento das plântulas, mas também porque é crucial para o recrutamento de espécies autocóricas em locais que são desfavoráveis para o estabelecimento das plântulas de espécies zoocóricas e anemocóricas. Finalmente, nossos resultados mostram que a dormência e o comportamento germinativo não diferirem entre fisionomias de cerrado, de lenhosas a herbáceas, o que indica que a sazonalidade climática é um filtro forte para a germinação e estabelecimento das plântulas ao longo das vegetações do cerrado, e respondem de forma similar à sazonalidade climática independentemente do habitat.

Palavras-chave: Dormência, nicho térmico de germinação, sazonalidade, heterogeneidade ambiental, savana Neotropical, mecanismos de redução de risco.

Abstract

Seed germination and seedling establishment are the initial and crucial stages of a plant's life cycle and are important in determining plant community dynamics and plant distribution and diversity patterns. In seasonal environments, water availability in the soil and environmental heterogeneity are the main factors that limit seed germination and seedling establishment. In these environments, seed dispersal season, germination niche, and dormancy synchronize germination with the onset of the rainy season, which maximizes the favorable period for seedling establishment and increases the chances of seedlings surviving the subsequent dry season. Plants respond to environmental heterogeneity by distributing germination through space and time. Distributing seeds throughout different areas (spatial dispersal) increases the chances that at least some will arrive in sites adequate for germination and establishment. On the other hand, dormancy increases the variation in germination time, distributing germination into multiple reproductive events (temporal dispersal), thus decreasing the likelihood that all seedlings die due to unpredictable events. However, most studies addressing the mechanisms that synchronize germination with the onset of the rainy season in seasonal tropical environments do not consider germination niche or species evolutionary history and are mainly focused on forest ecosystems. Therefore, a clear understanding on the relative importance of the mechanisms controlling germination time, on the interaction between these mechanisms, and on how they might be affected by life history traits and evolution is still lacking in seasonal tropical environments. Moreover, the role dormancy plays as a mechanism to face environmental heterogeneity has not been thoroughly explored in seasonal environments. Thus, in this thesis, I evaluated the mechanisms that cerrado plants use to synchronize germination with the onset of the rainy season and to face environmental heterogeneity. I also analyzed how such mechanisms vary in relation to plants functional and evolutionary characteristics. For such, dormancy and the thermal germination niche of 82 cerrado plant species, belonging to 26 families and including several growth forms, were determined from germination experiments. Additionally, dispersal syndrome, dispersal season, and seed mass were also determined for each species. Our results show that dormancy is an adaptative characteristic in cerrado as it increases the chances of seedling establishment by synchronized germination with the onset of the rainy season and by distributing the risk of recruitment of species with limited spatial dispersal (i.e., authochorous). Our results also demonstrate that dormancy is evolutionarily correlated with spatial dispersal, but not with seed mass or dispersal season, indicating there is a trade-off between spatial and temporal dispersal. Furthermore, dormancy and germination niche are alternative mechanisms used to face seasonality, and the relative importance of these mechanisms varies with dispersal season. Hence, dormancy is key to understanding the great plant diversity found in cerrado, not only because it increases the chances for seedling establishment, but also because it is crucial for the successful recruitment of autochorous species in sites that are unfavorable for the establishment of zoochorous and anemochorous species. Finally, our results show that plant species from closed to open cerrado physiognomies show similar germination traits and proportion of dormancy, suggesting that seasonality is a strong filter for both germination and seedling establishment throughout the cerrado plant communities and other seasonally dry ecosystems.

Keywords: Dormancy, thermal germination niche, seasonality, environmental heterogeneity, Neotropical savanna, risk reduction mechanisms

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INTRODUÇÃO GERAL

Sementes e plântulas estão envolvidas em vários fenômenos ecológicos que vão desde processos populacionais como persistência, dispersão e variabilidade genética até processos envolvendo comunidades vegetais e paisagens como colonização, sucessão e regeneração natural (Vázquez-Yanes & Orozco-Segovia, 1993; Grime & Hillier, 2000; Dalling, 2002). Portanto, a biologia das sementes é essencial para compreender padrões de distribuição, abundância, diversidade e dinâmicas das comunidades de plantas em diferentes escalas ecológicas (Marques et al., 2014). Além disso, o sucesso dos esforços de restauração ecológica e manejo florestal dependem do conhecimento da germinação de sementes e estabelecimento de plântulas (Khurana & Singh, 2001; Ladoucer et al., 2018).

Nas regiões tropicais com clima estacional, onde as estações seca e chuvosa são bem definidas, a disponibilidade de água no solo e a heterogeneidade espacial e temporal do ambiente são os principais fatores limitantes para a germinação e estabelecimento das plântulas (Ray & Brown, 1995; Franco, 2002; Marod et al., 2002; Viera et al., 2008; Salazar et al., 2012, Baskin & Baskin, 2014). A sazonalidade climática restringe o período favorável para o estabelecimento à estação chuvosa. Portanto, sincronizar a germinação com o início desta estação permite que as plântulas aproveitem ao máximo o período de estabelecimento, incrementando a chance de sobrevivência das plântulas à subsequente estação seca (Frankie et al., 1974; Garwood, 1983; Franco, 2002; Oliveira, 2008, Ramos et al., 2017). Por outro lado, períodos curtos e imprevisíveis de seca durante a estação chuvosa e a grande variação espacial na qualidade de lugares para germinar podem levar a uma limitação de recrutamento dada a baixa disponibilidade de condições adequadas para o estabelecimento das plântulas (Engelbrecht et al., 2006; Viera et al., 2008; Salazar et al., 2012). Desta forma, a distribuição espacial e/ou temporal das plântulas seria selecionada como uma forma de enfrentar a heterogeneidade ambiental (Buoro & Carlson, 2014).

As espécies de ambientes sazonais podem sincronizar a germinação com o começo da estação chuvosa através da **fenologia** de dispersão, a **dormência** ou variações na amplitude de **nicho de germinação** (Garwood, 1983; Donohue, 2005; Sautu et al., 2007; Salazar et al., 2011, Ramos et al., 2017, Fernandez-Pascual et al., 2017; definição e detalhes dos conceitos em negrito no glossário). Já que os ambientes sazonais apresentam uma variação climática previsível, uma forma comum de otimizar o momento de germinação nestes ambientes é sincronizar a dispersão das sementes com o começo da estação chuvosa e germinar logo após da dispersão (Garwood, 1983; Oliveira, 2008; Baskin & Baskin, 2014; Silveira et al., 2012; Ramos et al., 2017). Por outro lado, sementes dispersas em estações cujas condições climáticas não são adequadas para o estabelecimento das plântulas tendem a apresentar dormência, a qual adia a germinação até o começo da próxima estação chuvosa (Garwood, 1983; Probert, 2000; Salazar et al., 2011; Silveira et al., 2012; Baskin & Baskin, 2014; Ramos et al., 2017). Uma alternativa à dormência é apresentar requerimentos germinativos (i.e., nicho de germinação) muito específicos, que coincidem com as condições ambientais da estação favorável para o estabelecimento das plântulas e evitam a germinação durante os períodos desfavoráveis (Grubb, 1977; Donohue, 2005; Baskin & Baskin, 2014; Fernandez-Pascual et al., 2017).

As plantas enfrentam a heterogeneidade ambiental incrementando a dispersão espacial das sementes ou distribuindo a germinação no tempo (i.e., dispersão temporal) (Snyder, 2006; Buoro & Carlson, 2014). Ao distribuir as sementes ao longo de diferentes áreas, aumenta a chance de que pelo menos uma parte das sementes chegue a lugares adequados para a germinação e estabelecimento das plântulas (Buoro & Carlson, 2014; Rubio de Casas et al., 2015). Por outro lado, distribuir a germinação temporalmente, e consequentemente, o estabelecimento das plântulas em vários eventos durante a estação chuvosa ou entre anos, diminui a probabilidade de que todas as plântulas morram devido a eventos imprevisíveis (e.g. períodos de seca durante a estação chuvosa) (Buoro & Carlson, 2014; Baskin & Baskin, 2014). As plantas conseguem distribuir a germinação no tempo por meio da dormência, a qual incrementa a variação do tempo de germinação das sementes (Simons & Johnston, 2006; Venable, 2007; Baskin & Baskin, 2014). A dispersão espacial e temporal são vistas como mecanismos alternativos que diminuem o risco de uma falha reprodutiva total (i.e., todas as sementes morram), o que implica uma correlação negativa entre ambos mecanismos (Buoro & Carlson, 2014).

Os estudos a nível de comunidade dos mecanismos que sincronizam a germinação com o início da estação chuvosa nos ambientes tropicais sazonais não levam em consideração o nicho de germinação, e estão focados majoritariamente nos ecossistemas florestais (e.g., Ng, 1978; Garwood, 1983; Blakesley et al., 2002; Sautu et al., 2007; Yang et al., 2013). Além disso, os escassos estudos desenvolvidos nas savanas são filogeneticamente restritos (Salazar et al., 2011; Silveira et al., 2012; Ramos et al., 2017) e não abrangem as diferentes classes de dormência, síndromes de dispersão, nem a variação em traços funcionais como o peso das sementes. Portanto, não temos uma clara compreensão da importância relativa e da interação dos diferentes mecanismos que controlam o tempo de germinação nos ambientes sazonais tropicais, nem de como são afetados por outras características da história natural e evolutiva das espécies. Além disso, o papel da dormência (i.e., dispersão temporal) como mecanismo para enfrentar a heterogeneidade ambiental tem sido pouco explorado nos ambientes sazonais (Rubio de Casas et al., 2017).

Desta forma, o objetivo geral desta tese foi avaliar os mecanismos que as plantas do cerrado utilizam para sincronizar a germinação com o início da estação chuvosa, e para enfrentar a heterogeneidade ambiental, e como variam tais mecanismos em relação a características funcionais (e.g., peso das sementes, forma de crescimento) e evolutiva das espécies. A tese está dividida em três capítulos, sendo que no primeiro determinamos a importância relativa da dormência e da estação de dispersão como mecanismos que sincronizam a germinação com o início da estação chuvosa, e a relação entre síndrome de dispersão, dormência e fenologia da dispersão numa comunidade de cerrado lenhoso. No segundo capítulo, avaliamos o valor adaptativo da dormência em ambientes sazonais usando o cerrado lenhoso e campestre como estudo de caso, abrangendo as principais linhagens de angiospermas e um amplo espectro de formas de crescimento. Para tal, testamos a correlação evolutiva entre dormência, síndrome de dispersão, fenologia da dispersão e peso das sementes; a capacidade da dormência e do nicho de germinação como mecanismo alternativos para sincronizar a germinação com o início da estação chuvosa, e se a importância relativa destes mecanismo varia com a estação de dispersão; e a importância da dormência como mecanismo de redução de risco nos ambientes sazonais e como se correlaciona com a dispersão espacial das sementes. No terceiro capítulo, avaliamos se as espécies de fisionomias fechadas de cerrado (cerrado lenhoso ou stricto sensu) diferem de espécies de cerrado aberto (campo limpo, sujo e úmido) em termos da germinação, peso das sementes, dormência, fenologia e síndrome de dispersão, e forma de crescimento.

Glossário

A **fenologia** vegetal é a ciência ambiental focada em monitorar, compreender e predizer em que momento ocorrem eventos biológicos recorrentes no ciclo de vida, como a frutificação de populações de plantas (Morellato et al., 2016). Portanto, a fenologia da dispersão de sementes descreve em que momento os indivíduos de uma espécie ou as espécies numa comunidade estão dispersando as sementes.

O **nicho de germinação**, foi definido por Grubb (1977) como a gama de condições ambientais nas quais uma planta pode completar a transição de semente a plântula. O nicho de germinação geralmente é caracterizado em termos da temperatura e umidade que as sementes requerem para germinar (Fernandez-Pascual et al., 2017).

A **dormência** é um bloqueio inato nas sementes que restringe a gama de condições na qual podem germinar (Vleeshouwers et al., 1995; Finch-Savage & Leubner-Metzger, 2006; Thompson & Ooi, 2010), já que modifica a sensibilidade das sementes aos fatores ambientais que promovem a germinação (Thompson & Ooi, 2010). Portanto, a germinação no campo depende dos requerimentos germinativos, que são controlados pelo do grau de dormência, e das condições ambientais no momento (Vleeshouwers et al., 1995). A dormência otimiza a distribuição da germinação no tempo numa população, ao reduzir a chance de germinar sob condições ambientais desfavoráveis para o estabelecimento das plântulas, pospondo a germinação até períodos favoráveis para o estabelecimento (Vleeshouwers et al., 1995; Andersson & Milberg, 1998; Finch-Savage & Leubner-Metzger, 2006).

A dormência diminui a porcentagem de germinação e incrementa o tempo que as sementes demoram para germinar e aumenta a variação do tempo de germinação entre indivíduos (Baskin & Baskin, 2014; Batlla & Benech-Arnold, 2015). A quebra da dormência amplia a gama de condições ambientais na qual a semente é passível de germinar, aumentando a porcentagem, velocidade e sincronia de germinação (Baskin & Baskin, 2014; Batlla & Benech-Arnold, 2015). Desta forma, sementes sem dormência germinam rapidamente e sob uma amplia gama de condições ambientais, enquanto sementes dormentes apresentam um atraso na germinação, a qual acontece numa gama estreita de condições ambientais, ou não acontece (Baskin & Baskin, 2014; Batlla & Benech-Arnold, 2015). Na prática, entretanto, a quantidade limitada de sementes de espécies silvestres dificulta testar a presença de dormência pelo aumento na gama de condições na qual as sementes conseguem germinar. Assim sendo, o atraso na germinação de sementes incubadas sob condições ótimas tem sido usado como evidência de dormência em estudos ecológicos em diversas comunidades vegetais ao redor do mundo (Ng, 1978; Garwood, 1983; Blakesley et al., 2002; Salazar et al., 2011; Silveira et al., 2012; Yang et al., 2013). Entretanto, informações sobre a permeabilidade do tegumento e morfologia do embrião também fornecem valiosas informações sobre a classificação da dormência.

Deste modo, a dormência pode ser definida como a falha temporal de uma semente viável para germinar sob uma combinação de fatores ambientais favoráveis para sua germinação (Bewley et al., 2013). O problema desta definição é quanto deve durar a falha temporal na germinação para ser considerada dormência, e neste sentido Baskin e Baskin (2014) propõem que sementes incubadas sob condições ótimas de germinação que demorem mais de 30 dias em germinar apresentam dormência.

O sistema de classificação de dormência de sementes de Nikolaeva (2004), modificado por Baskin e Baskin (2014), é ecofisiologicamente abrangente, amplamente usado e reflete o fato que a dormência é determinada por características morfológicas e fisiológicas das sementes (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006, Leubner-Metzger et al., 2010). O sistema de classificação de Baskin e Baskin (2014) separa as espécies como não dormentes ou pertencendo a uma de cinco classes de dormência: Fisiológica, morfológica, morfofisiológica, física e fisiofísica.

As sementes com dormência fisiológica são permeáveis à água, e apresentam um potencial de crescimento do embrião muito baixo para conseguir expandir-se e superar a restrição mecânica dos tecidos ao redor. Nestas sementes, o balanço entre giberelina e ácido absícico modifica o potencial de crescimento do embrião controlando a perda ou manutenção da dormência (Bewley et al., 2013; Baskin & Baskin, 2014). Apresentam dormência morfológica as sementes cujos embriões estão diferenciados, mas não estão totalmente desenvolvidos tendo que crescer dentro da semente antes de germinar, o processo de crescimento do embrião e germinação tende a ser menor a 30 dias (Bewley et al., 2013; Baskin & Baskin, 2014). A dormência física é causada por camadas de células em paliçada impermeáveis a água na testa ou nas paredes do fruto, junto com as aperturas calazal e micropilar hermeticamente fechadas (Baskin & Baskin, 2014). As sementes com dormência morfofisiológica têm embriões pouco desenvolvidos, diferenciados e com dormência fisiológica, tardando em germinar mais do que as sementes com dormência morfológica (Leubner-Metzger, 2006; Baskin & Baskin, 2014). Finalmente, sementes com envoltórios impermeáveis e embriões fisiologicamente dormentes apresentam dormência fisiofísica (Baskin & Baskin, 2014).

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CAPÍTULO 1

Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality

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Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality

Background and Aims The relationship between fruiting phenology and seed dispersal syndrome is widely recognized, however, the interaction of dormancy classes and plant life-history traits in relation to fruiting phenology and seed dispersal are understudied. Here, was examined the relationship between fruiting season and seed dormancy and how such relationship is modulated by dormancy classes, dispersal syndromes, seed mass and seed moisture content in a Brazilian savanna (cerrado).

Methods Was experimentally determined dormancy classes (non-dormant, physical, morphological, morphophysiological, physiological, and physiophysical dormancy) of 34 cerrado species. Was also determined their seed dispersal syndrome (autochory, anemochory, zoochory), dispersal season (rainy, dry, rainy-to-dry and dry-to-rainy transitions), seed mass and moisture contents, and the estimated germination date. Were used log-linear models to evaluate how dormancy and dormancy classes are related to dispersal season and syndrome.

Key Results Proportion of dormant and non-dormant species was similar in cerrado. The community estimated germination date was seasonal, occurring at the onset of rainy season. Overall, anemochorous non-dormant species released seeds during the dry-to-rainy transition; autochorous physically-dormant species dispersed seeds during the dry season and rainy-to-dry transition; zoochorous species dispersed non-dormant seeds during the dry and rainy seasons, while morphological, morphophysiological or physiological dormant species dispersed seeds in the transitional seasons. Seed mass differed among dispersal seasons and dormancy classes, but seed moisture content did not vary with dispersal syndrome, season, or dormancy classes.

Conclusions The beginning of the rainy season was the most favorable period for seed germination in cerrado, and the germination phenology was controlled by both timing of seed dispersal and seed dormancy. Dormancy class was influenced by dispersal syndrome and season. Moreover, dormancy avoids seed germination during the rainy-to-dry transition, independently of dispersal syndrome. The variability of dormancy classes with dispersal syndrome allowed animal-dispersed species to fruit all year-round, but seeds germinate only during the rainy season. Conversely, seasonally restricted wind-dispersal species dispersed and germinated their non-dormant seeds only in the rainy season.

Key words: Cerrado; Dispersal syndromes; Dormancy classes; Fruiting phenology; Germination phenology; Neotropical savanna.

INTRODUCTION

In tropical regions with seasonal climate, water availability in the soil is the main factor limiting seedling establishment and growth (Ray and Brown, 1995; Franco, 2002; Baskin and Baskin, 2014). Seasonality affects patterns of seed production and seed germination, as well as seedling development and survival, and the period favoring plant growth is restricted to the rainy season, when seed germination and seedling establishment are most likely to occur (Garwood, 1983; Khurana and Singh, 2001; Oliveira, 2008; Salazar *et al*., 2011). Thus, in such ecosystems, germinating at the beginning of the rainy season is a characteristic that has evolved independently in many lineages (Garwood, 1983; Blakesley *et al*., 2002; Sautu *et al*., 2007; Oliveira, 2008; Salazar *et al*., 2011; Ramos *et al*., 2017), and is crucial for plant recruitment as it maximizes the favorable period for establishment, allowing seedlings to develop an efficient root system or to store enough resources to survive the subsequent dry season (Franco, 2002; Oliveira, 2008).

In seasonal tropical ecosystems, the time when seeds germinate is regulated by the relationship between fruiting phenology and seed dormancy. In general, species that disperse seeds at the beginning of the rainy season have non-dormant seeds that germinate quickly given that the soil moisture content for seedling development is adequate (Silveira *et al*., 2012, Ramos *et al*., 2017). However, seeds dispersed at the end of the rainy season and beginning of the dry season, a period during which the climatic conditions for seedling establishment are inadequate (but moisture still allows seed germination), are generally dormant and germinate only at the onset of the subsequent rainy season (Garwood, 1983; Probert, 2000; Blakesley *et al*., 2002; Sautu *et al*., 2007; Salazar *et al*., 2011; Ramos *et al*., 2017). Even though seed dormancy is considered the main mechanism controlling the timing of seed germination in seasonal ecosystems (Baskin and Baskin, 2014), a few studies carried out at the community level have suggested that seed germination is controlled by both seed dormancy and seed dispersal period (Garwood, 1983; Blakesley *et al*., 2002; Sautu *et al*., 2007; Salazar *et al*., 2011).

Seed dormancy is related to fruiting phenology, but it also depends on other characteristics of the species life history, such as seed dispersal syndromes, seed mass and phylogeny, which are essential to understand the evolutionary ecology of seed dormancy (Wang *et al.*, 2009; Yang *et al.*, 2013, Dayrell *et al.*, 2017; Ramos *et al.*, 2017). The few studies that have quantified dormancy classes at the community level and its relationships with life-history characteristics and seed traits have shown that seeds dispersed during the dry season usually have low moisture contents and physical dormancy, while those dispersed late in the rainy season have high moisture contents, physiological dormancy and are animal-dispersed (Sautu *et al.*, 2006, 2007; Salazar *et al.*, 2011).

The relationship between fruiting phenology and dormancy in the tropics has been tested at the community level for forest ecosystems (Ng, 1978; Garwood 1983; Blakesley *et al.*, 2002; Sautu *et al.*, 2007; Yang *et al.*, 2013), but studies in savannas are scarce, mostly restricted to certain clades (Silveira *et al.*, 2012; Ramos et al., 2017) or species (Salazar *et al.*, 2011), hindering the understanding of general regeneration patterns for this biodiversity hotspot. Moreover, such studies are deficient as they do not consider different dormancy classes and dispersal syndromes. Therefore, the relationship between dormancy classes and both life-history characteristics of species (e.g. dispersal season and dispersal syndrome) and seed traits (e.g. seed mass and seed moisture content) are not fully understood for savannas, which may or may not follow the patterns described for other seasonal ecosystems (Sautu *et al.*, 2007).

Here, we presented the first comprehensive study addressing the ecology of seed dormancy in a woody cerrado community, aiming to evaluate the relationship between fruiting phenology and seed dormancy and how such relationship is modulated by dormancy classes, dispersal syndromes, and seed mass and moisture content. Specifically, we aimed to: (1) evaluate the cerrado fruiting phenology at the community-level, using a unprecedented phenology database of 11 years to accurately estimate the dispersal season of each species; (2) estimate germination date of cerrado species and how it is affected by dispersal syndromes; (3) evaluate the proportion of dormant species in the community and how it varies according to dispersal season and syndrome; and (4) examine the relationship between dormancy classes, dispersal season and syndrome, and the seed mass and moisture content.

In seasonal tropical ecosystems, seed dormancy is related with the seed dispersal at the end of the rainy season and during the dry season or with limited seed dispersal (Garwood 1983; Sautu *et al.*, 2007; Wang *et al.*, 2009; Salazar *et al.*, 2011; Yang *et al.*, 2013; Ramos *et al.*, 2017). Therefore, we hypothesize that the proportion of dormant species in the cerrado depends on both fruiting phenology and dispersal syndromes. The cerrado fruiting patterns are characterized by ripe fruit production throughout the year, but a great proportion of species are fruiting at the end of the dry season and beginning of the rainy season (Tannus *et al*., 2006; Oliveira, 2008; Pirani *et al*., 2009; Silva *et al*, 2011; Camargo *et al*. 2013). Thus, we expect that the timing of seed dispersal and seed dormancy to be equally important in controlling the timing of seed germination in cerrado communities. Moreover, fruiting peak varies with dispersal syndrome, with anemochorous species showing a restrict dispersal season, limited to the end of the dry season, autochorous species fruiting mainly during the dry season, while zoochorous species fruiting all over the year, but peaking at the beginning of the rainy season (Batalha and Mantovani, 2000; Oliveira, 2008; Pirani *et al*., 2009). Consequently, we expect an interaction between dispersal syndrome and season to modulate seed dormancy. For example, zoochorous species that disperse seeds at the end of the rainy season should be dormant, anemochorous species dispersing seeds at the end of the dry season should have non-dormant seeds, whereas a vast number of autochorous species dispersing seeds during the dry season should be dormant (Wang *et al*., 2009; Yang *et al*., 2013; Ramos *et al*., 2017). Although the relationships between seed dormancy class and life-history characteristics are not fully understood for seasonal ecosystems, we expected that the cerrado community would show similar patterns as those described for other seasonal ecosystems. Therefore, we expected to find an interaction between dispersal during the dry season, physical dormancy and seeds with low moisture contents, while seeds dispersed late in the rainy season tend to show zoochoric dispersal, physiological dormancy and seeds with high moisture contents (Sautu *et al*., 2006, 2007; Salazar *et al*., 2011).

MATERIAL AND METHODS

Study area

The study was conducted in a private reserve area of 260 ha and 770 m altitude, located at Itirapina county, southeastern Brazil (22°10’ 52” S; 47°52’ 25”). The vegetation of the study area is predominately the cerrado *sensu stricto* (woodland savanna), characterized by a dominant woody layer (discontinuous tree canopy heights of approximately 7m) and a scattered herbaceous layer; for detailed description of vegetation structure and plant species composition see Reys *et al*. (2013). The climate is characterized by a dry season from April to September and a rainy season extending from October to March (Reys *et al*., 2013), with mean monthly temperatures of 18ºC in July and 32ºC in February, mean annual temperature of 20.7°C and mean total annual precipitation of 1524mm (Fig. 1a). The pattern of fruiting in the study area is characterized by ripe fruit production throughout the year, but fruiting peak varies with dispersal syndrome (Fig. 1b; Camargo *et al*. 2013). Fruiting of anemochorous species is concentrated at the end of the dry season, for autochorous species fruiting occurs mainly during the dry season, while for zoochorous species fruiting occurs all over the year, peaking at the beginning of the rainy season (database from Phenology Laboratory at UNESP, Fig. 1b).

Historical climatic data

We divided the year into seasons based on the analyses of 30 years of climatic information (1982-2012) from the Centro de Recursos Hídricos e Estudos Ambientais (CRHEA– EESC/USP) meteorological station, located about 6 Km away from the study site. The seasons were defined after a cluster analysis using Euclidian distance and unweighted pair-group average (UPGMA) carried out with the *Pvclust* package (Suzuki and Shimodaira, 2006) in R software (R Core Development Team, 2016). We used the mean and the coefficient of variation of the following variables for each month for the period of 30 years: maximum, minimum and mean temperatures, precipitation, number of rainy days, potential evapotranspiration, and precipitation minus potential evapotranspiration. Variables were standardized using the standard deviation. The values of potential evapotranspiration were calculated according to Thornthwaite and Mather (1955) and Rolim *et al*., (1998) with a field capacity of 100 mm.

The cluster analysis showed a high cophenetic coefficient (0.87) and divided the year into four seasons: rainy season (November to March), rainy-to-dry transition (April), dry season (from May to August), and dry-to-rainy transition (September to October; Fig. 2). The months during the dry season were characterized by low temperatures, low precipitation, few rainy days and low and variable evapotranspiration; the rainy season months were characterized by elevated temperatures, high precipitation, many rainy days and a significant difference between precipitation and potential evapotranspiration. The transitional months showed intermediate values between the dry and rainy seasons (Supplementary material S1).

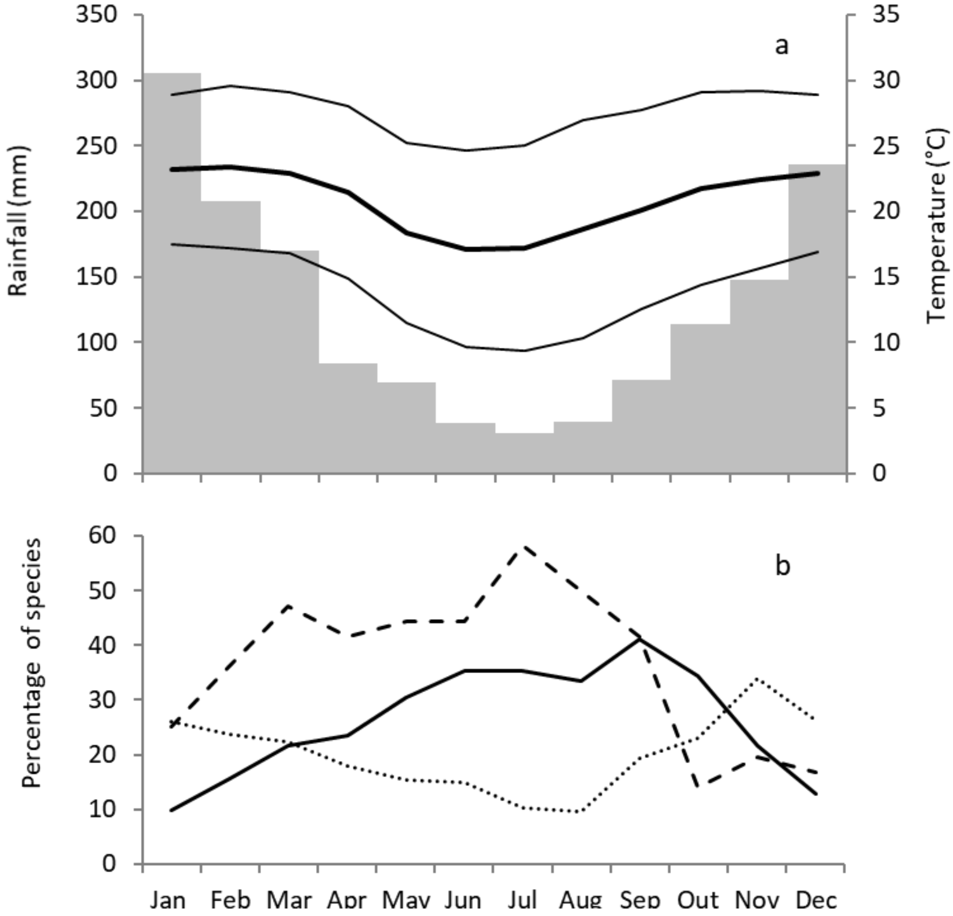

Figure 1. Climate and fruiting phenology for the cerrado study site at Itirapina, southeastern Brazil. (a) Average monthly temperatures and rainfall over a period of 30 years (1982-2012) (CRHEA– EESC/USP meteorological station). Maximum, mean and minimum temperature (solids lines), and rainfall (bars). (b) Percentage of species fruiting per month according to the seed dispersal syndrome based on the total of 73 species monitored (6 autochorous, dashed line; 17 anemochorous, solid line; and 50 zoochorous, dotted line) during 11 years of phenological observations (Phenology Laboratory at UNESP, unpublished).

Fruit and seed collection

Mature fruits were collected every 15 days from March 2015 to March 2016, from 34 species (Table 1). We randomly followed trails inside the reserve, collecting all fruiting species available. Fruits of at least 10 individuals per species were collected, except for *Qualea dichotoma*, *Virola sebifera* and *Kielmeyera coriacea,* for which we collected fruits of only one individual per species. Fruits of all individuals of a given species were put into paper bags and taken to the laboratory, where seeds were removed up to 48 hours after harvesting. Seeds were then dried for 48 hours at 25°C and 40% relative humidity. Seeds were kept stored in such conditions for less than three weeks prior to the germination experiments, except for seeds with moisture contents over 30%, in which germination experiments were set up to seven days after seeds were harvested.

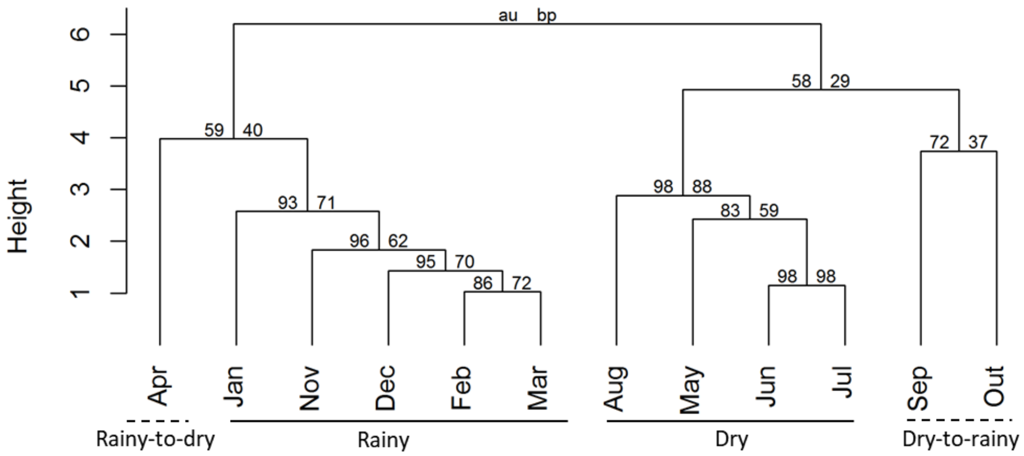

Figure 2. Dendrogram showing the months clustered by season according to the climatic variables used: rainy season from November to March, dry season from May to August, rainy-to-dry transition in April and dry-to-rainy transition from September to October. Data are the average for a period of 30 years (1982-2012) (CRHEA– EESC/USP meteorological station).

Dispersal syndrome

We used three sources to classify species dispersal syndromes: (1) morphological characteristics of the diaspore as proposed by Van der Pijl (1982); (2) information extracted from the literature (Morellato and Leitão-Filho, 1992; Oliveira and Moreira, 1992; Batalha and Mantovani, 2000; Weiser and Godoy, 2001; Camargo *et al*., 2013); and (3) field observations. The zoochorous species had fleshy fruits or fleshy structures partially or totally involving seeds; anemochorous species had winged or flat diaspores with a large area: volume ratio; autochorous species did not have fleshy structures neither did they show structures known to facilitate wind dispersal (Table 1).

Table 1. List of cerrado species sampled for the germination tests at Itirapina, southeastern Brazil, ordered by family and species names, the respective ecological and experimental information: seed collecting date, fruiting peak date (see methods for calculations), growth form (tree, shrub, forb), dispersal syndrome (zoochory, anemochory, autochory), dispersal season (Rainy = rainy season (Nov to Mar); Dry = dry season (May to Aug); Rainy-dry = rainy-to-dry season transition (April); Dry-rainy = dry-to-rainy season transition (Sept to Oct), dormancy class: ND = non-dormant; PD = physiological dormancy; PY = physical dormancy; MD = morphological dormancy; MPD = morphophysiological dormancy; and temperatures of the germination experiments which were set up according to seed availability.

Family	Species	Seed collecting date	Fruiting peak date	Growth form	Dispersal syndrome	Dispersal season	Dormancy class	Temperature (°C)
Annonaceae	*Xylopia aromatica* (Lam.) Mart.	April	April	Tree	Zoochory	Rainy-dry	MPD	25
Araliaceae	*Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi	October	September	Shrub	Zoochory	Dry-rainy	MD	15, 20, 25, 30, 35
Bromeliaceae	*Ananas ananassoides* (Baker) L.B.Sm.*	March	March	Herb	Zoochory	Rainy	MD	15, 20, 25, 30, 35
Calophyllaceae	*Kielmeyera coriacea* Mart. & Zucc.*	September	September	Shrub	Anemochory	Dry-rainy	ND	20, 25, 30
Erythroxylaceae	*Erythroxylum cuneifolium* (Mart.) O.E.Schulz	November	November	Shrub	Zoochory	Rainy	ND	25, 30
Fabaceae	*Anadenanthera falcata* var. falcata (Benth.) Altschul	October	September	Tree	Autochory	Dry-rainy	ND	15, 20, 25, 30, 35
Fabaceae	*Chamaecrista desvauxii* (Collad.) Killip*	April	April	Subshrub	Autochory	Rainy-dry	PY	15, 20, 25, 30, 35
Fabaceae	*Dalbergia misculobium* Benth.	May	August	Tree	Anemochory	Dry	ND	25
Fabaceae	*Dimorphandra mollis* Benth.	August	June	Tree	Autochory	Dry	PY	15, 20, 25, 30, 35
Fabaceae	*Machaerium acutifolium* Vogel	July	August	Tree	Anemochory	Dry	ND	20, 25, 30
Fabaceae	*Mimosa sommians* Humb. & Bonpl. ex Willd.*	April	April	Forb	Autochory	Rainy-dry	PY	25
Fabaceae	*Plathymenia reticulata* Benth.*	August	August	Tree	Anemochory	Dry	PY	15, 20, 25, 30, 35
Fabaceae	*Stryphnodendron* rotundifolium Mart.	August	August	Tree	Autochory	Dry	PY	15, 20, 25, 30, 35
Lauraceae	*Ocotea pulchella* (Nees & Mart.) Mez	November	October	Tree	Zoochory	Dry-rainy	ND	25
Loganiaceae	*Strychnos* sp.*	October	October	Shrub	Zoochory	Dry-rainy	PD	20, 25, 30
Malpighiaceae	*Byrsonima intermedia* A.Juss.	April	February	Shrub	Zoochory	Rainy	PD	25

Melastomataceae	*Leandra solenifera* (DC.) Cogn.	November	December	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia albicans* (Sw.) Triana	November	December	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia chamisois* Naudin *	September	September	Shrub	Zoochory	Dry	ND	20, 25, 30
Melastomataceae	*Miconia fallax* DC.	November	November	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia ligustroides* (DC.) Naudin	March	March	Tree	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia rubiginosa* (Bonpl.) DC.	March	March	Tree	Zoochory	Rainy	ND	20, 25, 30
Myristicaceae	*Virola sebifera* Aubl.	October	October	Tree	Zoochory	Dry-rainy	MPD	15, 20, 25, 30, 35
Myrtaceae	*Myrcia guianensis* (Aubl.) DC.	November	November	Tree	Zoochory	Rainy	ND	15, 20, 25, 30, 35
Myrtaceae	*Myrcia splendens* (Sw.) DC	January	January	Tree	Zoochory	Rainy	ND	25
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze	May	November	Tree	Zoochory	Rainy	PD	15, 20, 25, 30, 35
Rubiaceae	*Amaioua guianensis* Aubl.	July	June	Tree	Zoochory	Dry	ND	15, 20, 25, 30, 35
Rubiaceae	*Palicourea rigida* Kunth	March	March	Shrub	Zoochory	Rainy	PD	25
Rubiaceae	*Psychotria hoffmannseggiana* (Willd. ex Schult.) Müll.Arg *	April	April	Forb	Zoochory	Rainy-dry	PD	15, 20, 25, 30, 35
Rubiaceae	*Coccocypselum* sp.*	April	April	Forb	Zoochory	Rainy-dry	PD	15, 20, 25, 30, 35
Siparunaceae	*Siparuna guainensis* Aubl.	March	February	Shrub	Zoochory	Rainy	PD	25
Vochysiaceae	*Qualea dichotoma* (Mart.) Warm.*	July	July	Tree	Anemochory	Dry	ND	20, 25, 30
Vochysiaceae	*Qualea grandiflora* Mart.	September	September	Tree	Anemochory	Dry-rainy	ND	15, 20, 25, 30, 35
Vochysiaceae	*Vochysia tucanorum* Mart	September	September	Tree	Anemochory	Dry-rainy	ND	20, 25, 30

*Species for which the fruiting peak and dispersal season were determined according to the seed collecting date. For the remaining species, dispersal season refers to the mean fruiting peak date determined based on 11 years of phenological data from the study site (see Methods for details).

Fruiting phenology

A long-term phenological study has been conducted by the Phenology Laboratory at UNESP since September 2004 in 36 25 x 2 m transects established throughout the study site with a distance of at least 50m from each other (Reys *et al*., 2013, Camargo *et al*., 2013). In each transect, all individuals with circumference at 30 cm from ground level >3cm were tagged and have been monitored for changes on reproductive and vegetative phenology at monthly intervals. The intensity of the phenophase for each tagged individual was registered using a semi-quantitative index with three classes: 0 (absence), 1 (up to 50% of branches with ripe fruits) and 2 (>50% of branches with ripe fruits) (Opler *et al*., 1976, Vogado *et al*., 2016).

For 24 out of the 34 species collected in the present study, the fruiting peak was determined based on the 11-years database (2005-2015) detailed above. The mature fruiting peak date of each of those 24 species was defined as the month with the maximum number of individuals fruiting (scores >1) or with the higher score sum. For the remaining species, the fruiting peak was determined based on the dates of the seed collection, carried out fortnightly throughout 2015-2016 (Tab. 1). The fruiting peak date was therefore used to classify the species seed dispersal season as the dry season, rainy season, and dry-to-rainy, or rainy-to-dry transitions.

Data regarding the fruiting phenology of all species were then analyzed using circular statistical parameters, where we considered the years of phenological observation as independent and the date or month of fruiting peak as the phenological variable. All analyses follow the procedures described by Morellato *et al*. (2000, 2010). Given that the circular data are a scale with no true zero (Zar, 1999), the month of peaking fruiting was converted to angles, where January corresponds to the 30^o degree circular interval and is assigned the 15^o and so on up to December, corresponding to the last interval of 330^o or 345^o. We estimated the average fruiting peak date or the average angle for each species based on the frequency of fruiting peak dates each month over 11 years. The mean angle corresponds to the mean date of the year around which most individuals had mature fruiting peak (Morellato *et al*., 2010). With the average fruiting peak date for each species we calculated the average angles for the community (34 species) and for each dispersal syndrome. The Rayleigh test was applied to determine significance of the average angle (Zar, 1999). When significant, we can infer the occurrence of a seasonal pattern, since the Rayleigh test is confirming that fruiting peaks are significantly clustered around the average angle (here representing a month of the year), and we use the length of the *r* vector to infer the degree of seasonality (Morellato *et al*., 2000, 2010). The *r* vector has no unit and ranges from 0, for no concentration around the mean date (no seasonality) to 1, for all unities concentrated at the same date (the highest degree of seasonality). The analyses were carried out with the Oriana 4 software (Kovach, 1994).

Classification of seed dormancy

For the germination experiments, seeds were placed in Petri dishes with two layers of filter paper saturated with distilled water under 24 hours white light (≈32 μmol/m^{2}s), and up to five constant temperatures (Table 1). For each species, we used six replicates containing 20-25 seeds in each temperature according to seed availability. Germination was determined by radicle curvature or protrusion of aerial structures (e.g. cotyledons or plumules; Northam and Callihan, 1994). The experiments were monitored three times a week for one month, after which the germination was monitored weekly for a maximum of 12 months or until the germination curve was stabilized (at least 4 weeks without germination; Sautu *et al*., 2006). At the end of the experiment, viability of non-germinated seeds was analyzed by means of the Tetrazolium test at 1% solution at 30°C for 48-72h (ISTA, 2007). The optimal temperature for germination for each species was determined as the temperature or array of temperatures with the highest germination percentage and germination rate. The percentage of germination, mean germination time and germination rate were calculated according to Ranal and Santana (2006).

We adopted the dormancy concept and classification system proposed by Baskin and Baskin (2014), where dormant seeds show one of the following characteristics: seeds with undifferentiated or undeveloped embryos, water impermeable diaspores, or seeds that when incubated under favorable environmental conditions for germination show a mean germination time greater than 30 days. Non-dormant seeds (ND) have a mean germination time of less than 30 days, water-permeable seed coats and totally developed embryos.

Dormancy classes

Species were classified as non-dormant (ND) or into five dormancy classes according to Baskin and Baskin (2014): Physical dormancy (PY), species with impermeable seed coats, well-developed and non-dormant embryos (germination occurs within 30 days after physical scarification); morphological dormancy (MD), species with seeds containing undeveloped embryos and a mean germination time of less than 30 days;

morphophysiological dormancy (MPD), seeds with undeveloped embryos and mean germination time over 30 days; physiological dormancy (PD), seeds that are permeable to water, with well-developed embryos and a mean germination time over 30 days; and physiophysical dormancy (PYPD), seeds that are impermeable to water and have physiological dormancy.

Seed permeability to water was determined by imbibition tests with intact, fresh seeds. One-hundred recently harvested seeds were weighed individually (when each seed had a weight of over 0.001g) or in six groups of 25 seeds each (for seeds weighing less than 0.001g). Seeds were then placed in germination boxes with two layers of filter paper saturated with distilled water and incubated at 25°C under white light for 48-72 hours. Another layer of filter paper saturated with distilled water was placed over the seeds in each germination box (ISTA, 2007). We registered the percentage increase in fresh weight (P%) for each seed or group of seeds for every time interval with the formula: $P\% = [(P2 - P1)/P1] \times 100$, where P1 and P2 represent the fresh weights for times t1 and t2, respectively, and thus, determined the percentage of seeds that did imbibe (Paiva *et al*., 2006; Orozco-Segovia *et al*. 2007; Sautu *et al*., 2007;). For species belonging to families or genera that knowingly have water impermeable seeds (Willis *et al*., 2014), we compared the percentage of imbibed seeds, germination percentage and mean germination time between intact seeds and mechanically scarified seeds. For species belonging to families or genera that have seeds with undeveloped embryos (Baskin and Baskin, 2014), we determined embryo growth before germination by comparing the embryo:seed size ratio of 20 seeds cut longitudinally: ten fresh seeds and ten seeds imbibed for 30 days.

Estimated germination date

The estimated germination date was determined differently for dormant and non-dormant species, given that non-dormant species that dispersed during the dry season and the dry-to-rainy transition germinated promptly under laboratory conditions, but the low soil moisture and temperature in the field during this period are most likely insufficient to stimulate germination (Goldstein *et al*., 2008; Ramos *et al*., 2017).

For dormant species, the estimated germination date was determined by adding the average fruiting peak date (see fruiting phenology) to the germination time for each species. The species germination time was calculated as the sum of the mean germination time in the optimum germination temperature with its standard deviation. For instance, the estimated germination date of a species with a seed dispersal peak in the beginning of June and a germination time of 90 days would be in the beginning of September. For species with non-dormant seeds, the estimated germination date was determined in two ways: for species dispersing seeds in the rainy season, we added the average fruiting peak date to the germination time for each species, and for species dispersing seeds in the dry season and the dry-to-rainy transition, we added the germination time for each species to the onset of the rainy season (beginning of November).

We only used the 28 species that had a germination percentage over 50% (Supplementary material S2), given that the mean germination time tends to be underestimated with low germination percentages. The estimated germination date was thus considered as the month where most seeds of that species would germinate. With the estimated germination date for each species we calculated the average estimated germination date (average angles) for the community and for each dispersal syndrome. The Rayleigh test was applied to determine significance of the average angle (Zar, 1999) and to infer the occurrence of seasonal patterns on germination timing as described above (Morellato *et al*., 2000, 2010).

Seed mass and moisture content

To determine the seed mass for each species, one-hundred recently harvested seeds were weighed individually (for seeds weighing over 0.001g) or in eight groups of 100 seeds each (for seeds weighing less than 0.001g). The moisture content was calculated using the formula: $MC\% = [(M2 - M3)/(M2 - M1)] \times 100,$ where M1= mass of the container, M2= mass of the container with fresh seeds, M3= mass of the container with dried seeds. The seeds were oven dried at 80°C until weight stabilization, for at least 72 hours, using two replicates of at least 1g each. Seeds larger than 1cm were cut before weighing (ISTA, 2007).

Data analyses

To examine if fruiting phenology, seed dormancy, and dispersal syndrome are related, we carried out two log-linear analyses. Log-linear models treat the cell frequencies as counts distributed as a Poisson random variable, and these models do not distinguish response and predictor variables; all the variables are considered equally as response variables (Quinn and Keough, 2002). One log-linear analysis was run to test whether seed dormancy (presence/absence) is related to dispersal season and dispersal syndrome (full model: ~Dormancy+ Dispersal season+ Dispersal syndrome+ Dispersal syndrome*Dormancy+ Dispersal syndrome*Dispersal season+ Dispersal season* Dormancy), and another to test the relationship between dormancy classes, dispersal season and dispersal syndrome (full model: ~Dormancy class+ Dispersal season+ Dispersal syndrome+ Dispersal syndrome*Dormancy class+ Dispersal syndrome*Dispersal season+ Dispersal season* Dormancy class).

In both analyses, first we contrasted all possible models (full and reduced models) and chose the models that had the lowest AIC and likelihood ratio (LR) values. We then tested which interactions in the chosen model were significant by contrasting all models of conditional interactions with the model of homogenous interactions (Quinn and Keough, 2002). All analyses were carried out using the package *MASS* (Venables and Ripley, 2002) in R software (R Core Development Team, 2016).

We conducted two factorial analysis of variance with permutations to evaluate the relationship of both seed moisture content and seed mass with dormancy class, dispersal season and dispersal syndrome; these analyses were done using the *lmPerm* package (Wheeler, 2010) in R software (R Core Development Team, 2016). *Post-hoc* Tukey's tests were performed for multiple comparisons among variables.

RESULTS

Life history and seed traits

Seeds from 34 species belonging to 28 genera and 16 families were sampled in the present study, including 31 woody species and three herbaceous species (Table 1). The proportion of cerrado dormant and non-dormant species was similar (47.1 and 52.9%, respectively). Zoochory was the most common dispersal syndrome (64.7%), followed by anemochory (20.6%) and autochory (14.7%; Fig. 3). Among the studied species, 38.2% dispersed their seeds during the rainy season, 14.7% in the rainy-to-dry transition, 20.6% during the dry season and 26.5% in the dry-to-rainy transition (Fig. 3).

Seed dispersal occurred throughout the year and no seasonal patterns were observed for the studied cerrado community (r=0.13; Rayleigh test p=0.585; Fig. 4a; Supplementary material S3). However, fruiting patterns differed according to dispersal syndrome (Fig. 4). For anemochorous species, fruiting peak was very seasonal, concentrated in August and September, at the end of the dry season and dry-to-rainy transition (r = 0.93; Rayleigh test p <0.001; Fig. 4b; Supplementary material S3). For autochorous species, fruiting peak was not significantly seasonal and occurred mainly from April to September, from the rainy-to-dry transition up to the dry-to-rainy transition (Fig. 4c; Supplementary material S3). Finally, zoochorous species also did not show a significantly seasonal pattern of peak fruiting, although seed dispersal was higher during the rainy season (Fig. 4d; Supplementary material S3).

The estimated germination date was significantly seasonal and occurred with the onset of the rainy season, between November and December, both at the community level (r = 0.56; Rayleigh test $p < 0.001$), for anemochorous (r = 0.96; Rayleigh test $p < 0.001$) and zoochorous species (r = 0,46; Rayleigh test $p < 0.031$) (Fig. 4; Supplementary material S4). Autochorous species did not show a significant seasonal pattern of germination dates, with germination occurring between August and December (Fig. 4, Supplementary material S4).

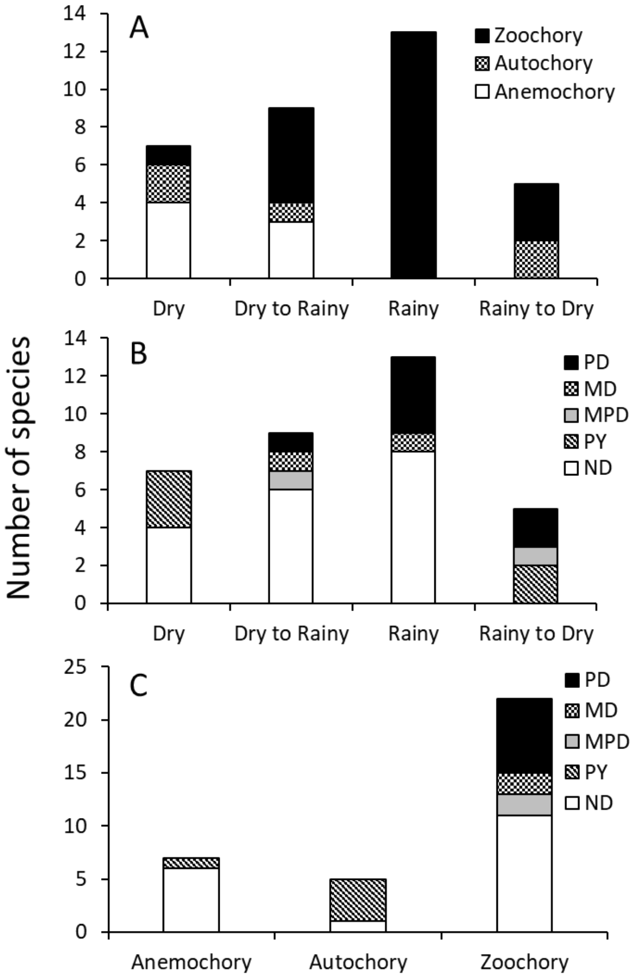

Figure 3. Number of species fruiting in each dispersal season according to (a) dispersal syndrome; (b) dormancy class; and (c) number of species in each dispersal syndrome according to dormancy class in a cerrado community, southeastern Brazil. Dormancy class: ND (Non-dormant), PY (Physical), MPD (Morphophysiological), MD (Morphological) and PD (Physiological).

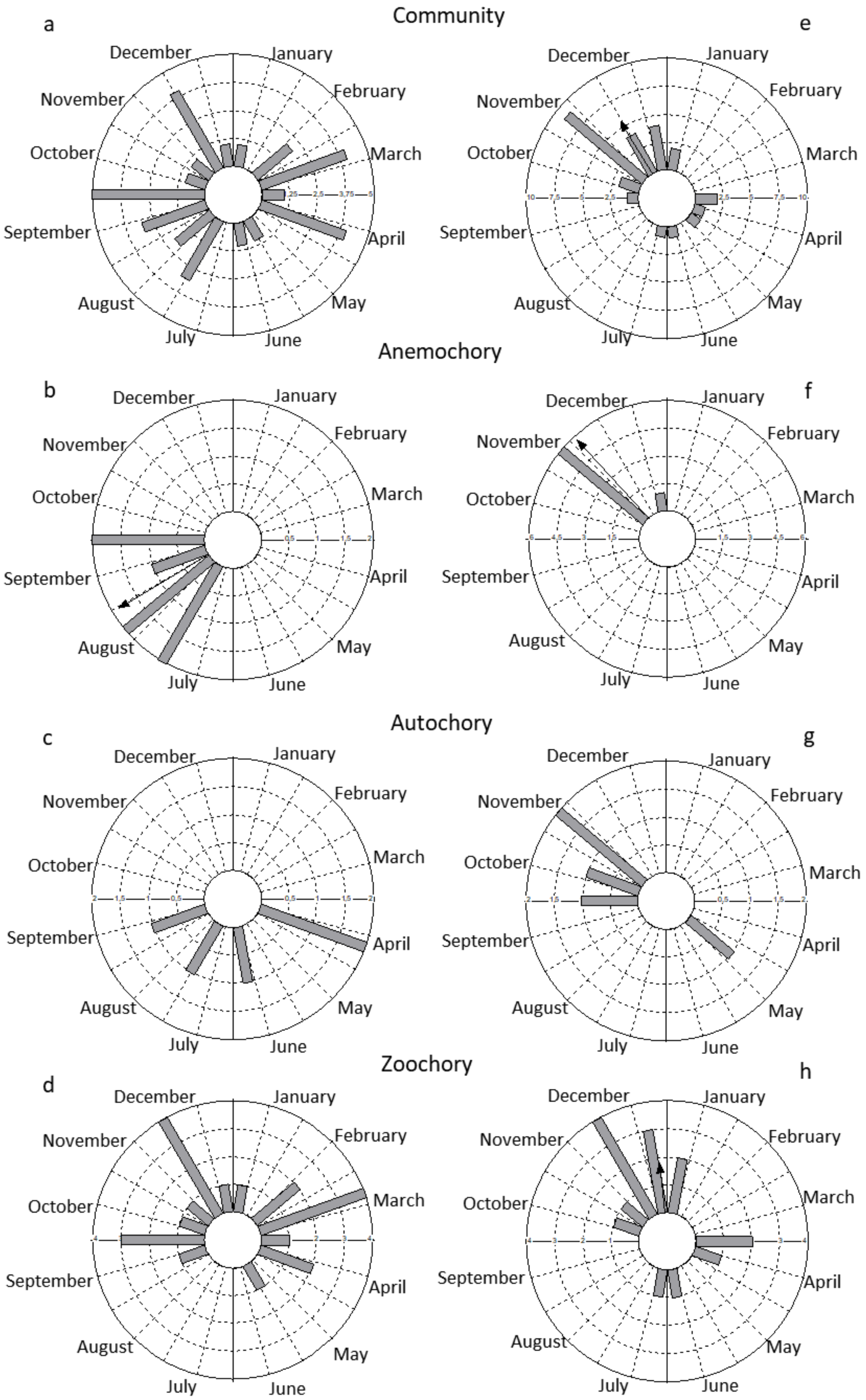

Figure 4. Circular histograms for the frequency of fruiting peak dates (a, b, c, d) and estimated germination dates (e, f, g, h) for the community and for each dispersal syndrome in a cerrado community, southeastern Brazil. The black arrow indicates the mean angle (mean date) and the arrow length corresponds to the mean vector (r) value. Circular histograms without black arrow indicate the mean angle was not significant (details in Methods and Tables S2 and S3).

Seed mass had a frequency distribution positively asymmetric (3.04) and concentrated (kurtosis 11.51), in which 82% of seeds weighed between 0.01 and 0.1g. Seed mass differed according to dispersal season and dormancy class but did not vary significantly with dispersal syndromes and interactions among traits (Supplementary material S5; Fig. 5a-c). Seeds dispersed during the dry season and the dry-to-rainy transition were heavier (mean seed mass of 0.067 and 0.193g, respectively) than those dispersed during the rainy season and the rainy-to-dry transition (mean seed mass of 0.021 and 0.014g, respectively; Tukey p <0.01; Fig. 5b). Species with MPD had a greater seed mass than those in other dormancy classes (Tukey p<0.05, Fig. 5a).

Seed moisture content showed an asymmetric distribution frequency (1.39) and positive kurtosis (0.69), with 70% of species having low moisture contents (<20%). Seed moisture content did not differ among dispersal syndromes, dispersal seasons, dormancy classes or any interaction among variables (Fig. 5d-f; Supplementary material S6).

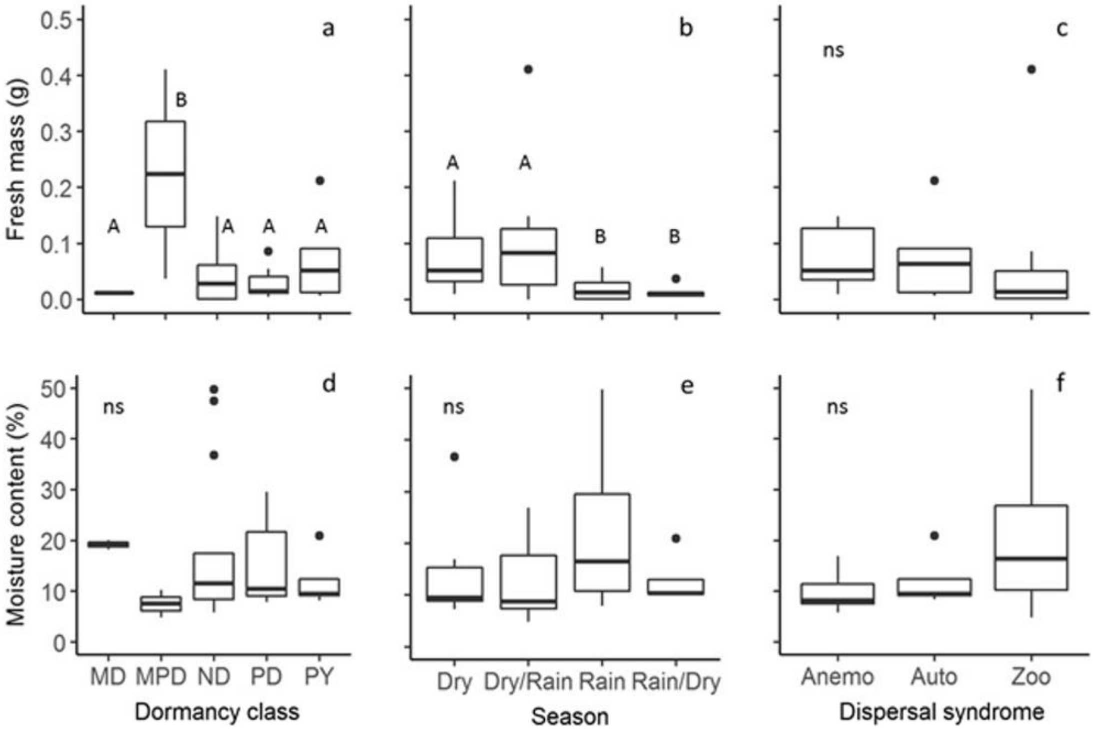

Figure 5. Relationship between seed mass (a, b, c) and moisture contents (d, e, f) according to dormancy class, seed dispersal season and dispersal syndrome for a cerrado community in southeastern Brazil. Different capital letters indicate significant differences (Tukey test p≤0.05), ns = not significant. Dormancy class: ND (Non-dormant), PY (Physical), MPD (Morphophysiological), MD (Morphological) and PD (Physiological). Anemo (Anemochory), Auto (Autochory), Zoo (Zoochory).

Relationships between seed dormancy, fruiting phenology and dispersal syndrome

The proportion of dormant species varied with dispersal season: 33.3% of species dispersing in the dry-to-rainy transition, 38.5% of species dispersing during the rainy season, 43% of species dispersing throughout the dry season, and all species dispersing in the rainy-to-dry transition had dormant seeds (Fig. 3).

The log-linear model (~Dormancy + Dispersal syndrome + Dispersal season+ Dispersal syndrome*Dispersal season), chosen according to the AIC and LR values (Table 2), and the contrasts between the conditional and homogenous association models (Table 3) indicated that dormancy was related to the interaction between dispersal syndrome and season. Thus, anemochorous species were related to absence of dormancy and dispersal during the dry season and the dry-to-rainy transition. For autochorous species, dispersal during the dry-to-rainy transition was related to absence of dormancy, while dispersal during the rainy-to-dry transition was related to dormancy. For zoochorous species, dispersal during the dry and rainy seasons was related to absence of dormancy and dispersal in the transitional seasons was related to dormancy, especially in the rainy-to-dry transition (Fig. 3 and Supplementary Material S7).

Table 2. The competing log-linear models tested to evaluate the relationship between seed dispersal season, dispersal syndrome and dormancy (presence/absence) for a cerrado community in southeastern Brazil.

Model	L.R.	df	P	AIC
1 Season+syndrome+dormancy	41.94	17	0.006	53.26
2 Season*syndrome+season*dormancy	**9.79**	**8**	**0.28**	**41.79**
3 Season*dormancy+ syndrome*dormancy	27.49	12	0.007	51.49
4 Season*syndrome+ syndrome*dormancy	12.69	9	0.177	42.69
5 Season*syndrome+season*dormancy+syndrome*dormancy	6.01	6	0.421	42.01
6 Full model (satured model)	0	0		48

The chosen model, with the lowest AIC and likelihood ratio (LR) values, is given in bold; d.f. = degrees of freedom.

Table 3. The hierarchical comparisons of models to determine the significant interactions between seed dispersal season, dispersal syndrome and dormancy (presence/absence) for a cerrado community in southeastern Brazil.

Term	Models compared	L.R.	df	P
Season*dormancy	4 vs 5	6.686	3	0.083
Syndrome*dormancy	2 vs 5	3.783	2	0.151
Season*syndrome	**3 vs 5**	**21.487**	**6**	**0.0015**

The significant conditional interaction, according to p values, is given in bold; L.R. = likelihood ratio; d.f. = degrees of freedom.

According to the log-linear model (~Dormancy class+ Dispersal season+ Dispersal syndrome+ Dispersal syndrome*Dormancy class+ Dispersal syndrome*Dispersal season), chosen by the AIC and LR values (Table 4), and the contrasts between the conditional and homogenous association models (Table 5), dispersal syndrome was related with dormancy class and dispersal season. MD, MPD and PD were present exclusively among zoochorous species, while PY was detected in anemochorous and autochorous species and ND species were found among all dispersal syndromes (Fig. 3). MD was related with dispersal during the dry-to-rainy transition, MPD to dispersal in both transitional seasons, especially rainy-to-dry transition, and PD to dispersal in the rainy-to-dry transition. In general, zoochorous species had a negative relationship between dispersing during the dry and rainy season and dormancy (MD, MPD and PD), and a positive relationship between dispersing in the rainy-to-dry transition and all dormancy classes, except MD (Fig. 3, Supplementary material S8). For autochorous species, PY was related to dispersing during the dry season and rainy-to-dry transition. Finally, for anemochorous species PY was related exclusively with dispersing during the dry season. For both anemochorous and autochorous species, we observed a positive relationship between dispersing in the dry-to-rainy transition and ND (Fig. 3, Supplementary material S8).

Table 4. The competing log-linear models tested to evaluate the relationship between seed dispersal season, dispersal syndrome and dormancy class for a cerrado community in southeastern Brazil.

Model	L.R.	Df	P	AIC
1 Season+syndrome+dormancy class	66.37	50	0.06	76.72
2 Season * syndrome + Season * dormancy class	16.52	32	0.989	72.52
3 Season * dormancy class + syndrome * dormancy class	14.35	30	0.993	74.35
4 Season * syndrome + syndrome * dormancy class	**17.24**	**36**	**0.997**	**65.24**
5Season*syndrome+Season*dormancyclass+syndrome* dormancy class	0.17	24	1	72.17
6 Full model (satured model)	0	0		120

The chosen model, with the lowest AIC and likelihood ratio (LR) values, is given in bold; d.f. = degrees of freedom.

Table 5. The hierarchical comparisons of models to determine the significant conditional interactions between seed dispersal season, dispersal syndrome and dormancy class for a cerrado community in southeastern Brazil.

Term	Models compared	L.R.	df	P
Season * dormancy class	4 vs 5	17.24	12	0.141
Syndrome * dormancy class	**2 vs 5**	**16.52**	**8**	**0.036**
Syndrome * season	**3 vs 5**	**14.35**	**6**	**0.026**

The significant conditional interactions, according to p values, are given in bold; L.R. = likelihood ratio; d.f. = degrees of freedom.

DISCUSSION

Our results indicated that seed dormancy was dependent of the interaction between a species dispersal syndrome and the seed dispersal season. Thus, species with limited dispersal (autochorous) tend to produce dormant seeds, while species with long-distance dispersal (anemochorous and zoochorous) presented dormant seeds only when dispersal occurred in unfavorable seasons, such as the rainy-to-dry transition. The harsh environmental conditions that follow seed dispersal likely reduce the probability of seedling establishment of cerrado species. Moreover, the relationship between dormancy and dispersal season was consistent among different dormancy classes, and varied with the dispersal syndrome. For instance, PY was related to anemochory and autochory, while MD, MPD and PD were related to zoochory. The proportion of species in our cerrado community dispersing dormant seeds during the dry season (43%) was similar to what is described for humid Tropical forests (Sautu, 2007). We also demonstrated that cerrado species germinate seasonally in the beginning of the rainy season, consistent with our expectations and other seasonal ecosystems (Garwood, 1983; Veenendaal *et al.*, 1996; Marod *et al.*, 2002; Blakesley *et al.*, 2002). We therefore suggest that germinating during the rainy season was selected across seasonal ecosystems, independent of phylogenetic groups, growth forms, dispersal syndrome or degree of seasonality. Further investigation including a larger number of species and growth forms are needed to test our assumption and investigate phylogenetic restrictions and the evolution of seed dormancy in cerrado.

Synchronizing germination with the onset of the rainy season, as observed at cerrado community and for anemochoric and zoochoric species, may increase plant success as it maximizes the first growth period, allowing seedlings to develop an efficient rooting system and/or to accumulate enough storage reserves in order to survive the subsequent dry season (Frankie *et al.*, 1974; Garwood, 1983; Franco, 2002; Oliveira, 2008). On the other hand, the lack of seasonal germination in autochorous species suggests that, for these cerrado species, dormancy was more related to distributing germination throughout the year rather than synchronizing germination with the most favorable period for seedling establishment. In fact, the results showed that the mean germination time of autochorous species was more variable than for anemochorous and zoochorous species (coefficient of variation of 29.4% versus 10.6 and 12.3%, respectively; Supplementary material S2), confirming that in species with limited seed dispersal distance, dormancy is more related to spreading germination through time. Such distribution of germination time across seasons might enhance the chances for seedling establishment in autochorous species by ensuring that germination of some seeds would occur when environmental conditions are suitable for seedling establishment, and by decreasing competition between sibling plants (Hyatt and Evans, 1998; Wang *et al*., 2009; Volis and Bohrer, 2013; Ramos *et al*., 2017).

The timing for seed germination in the cerrado community was controlled both by dispersal season (beginning of the rainy season) and by dormancy, differing from other studies in seasonal ecosystems (Jurado and Flores, 2005), including savannas (Baskin and Baskin, 2014), which recognize dormancy as the main mechanism controlling germination. The relatively lower percentage of dormant species in the community is consistent with other studies in open cerrado and seasonal grasslands which have also reported less than 50% of dormant species (Dayrell *et al*., 2016; Zupo, 2017; Ramos *et al*., 2017). The cerrado, unlike the semi-arid savannas of Africa (Veenendaal *et al*,. 1996) and Australia (Mott, 1978), is considered a mesic savanna with a highly predictable rainy season (Oliveira-Filho and Ratter, 2002), which allows the coexistence of both mechanisms: seed dispersal when climatic conditions are favorable for seedling establishment or delaying germination (dormancy) to a point in time when climatic conditions are suitable for seedling establishment (Freas and Kemp, 1983). Moreover, more than 50% of species in the community dispersed seeds between the end of the dry season and beginning of the rainy season, suggesting that the fruiting peak of cerrado species was related to the period in which seedling establishment and growth is most likely to succeed.

In the cerrado community, all species dispersing seeds in the rainy-to-dry transition were dormant, contrasting with less than 43% of dormant seed species dispersing in the other seasons. Additionally, the relationship between dormancy and dispersal during the rainy-to-dry transition was maintained by different dormancy classes, which varied with dispersal syndrome. The pattern just described suggests that dormancy in cerrado species is associated with dispersal season and that the dry season is a strong filter restricting seedling establishment. The climatic conditions (temperature and rainfall) during the rainy-to-dry transition could stimulate germination, but are unsuitable for seedling establishment, as it is a short and highly unpredictable period followed by a marked drought. Therefore, the evolution of dormancy in seeds dispersed throughout this period is favored, as it avoids germination during unfavorable conditions for seedling establishment (Jurado and Flores, 2005; Silveira *et al.*, 2012; Ramos *et al.*, 2017).

Furthermore, dormancy in cerrado species was mostly controlled by the interaction between dispersal season and dispersal syndrome, rather than by dispersal season or dispersal syndrome alone. Thus, species with limited dispersal (autochorous) tend to be dormant, while those with moderate to long dispersal (anemochorous and zoochorous) show dormancy when the seeds are dispersed during harsh conditions or periods of great climatic uncertainty. According to Venable and Lawlor (1980) and Freas and Keamp (1983), species with moderate dispersal dispersing seeds under predictable climatic conditions tend to be non-dormant, given that seeds will likely reach sites suitable for germination and establishment. On the other hand, dormancy is favored in species with limited dispersal, dispersing seeds during periods of great environmental uncertainty, as the odds of reaching sites suitable for germination are reduced (Cohen, 1968).

The expected interactions between dispersal during the dry season, low seed moisture content and physical dormancy, and also between dispersal during the rainy-to-dry transition, zoochory, high seed moisture content and physiological dormancy (see Sautu *et al.*, 2006, 2007; Salazar *et al.*, 2011) were partially corroborated in our work. Seed moisture content did not differ with dispersal syndrome, dispersal season or dormancy class, but species that had high moisture contents (>36%) were dispersed mainly during the rainy season and germinated quickly. The interaction between high moisture content, prompt germination and dispersal during the rainy season may be advantageous as it reduces the probability of seed desiccation and contributes to a faster seedling development during its initial growth period (Pritchard *et al.*, 2004). We observed, however, that most species (70%) had low seed moisture contents (less than 20%), a feature commonly found in environments with dry seasons, as in the cerrado, since seeds with low moisture contents usually tolerate dry periods better than those with high moisture contents (Murdoch and Ellis, 2000; Tweddle *et al.*, 2003; Pritchard *et al.*, 2004).

However, the relationship of dormancy class with dispersal syndrome was stronger than with dispersal season, given that dormancy allows seeds to avoid germinating during the rainy-to-dry transition and the mechanism used (dormancy class) varied with dispersal syndrome. Thus, in species with dry fruits (autochorous and anemochorous), the only mechanism avoiding germination is PY, while in species with fleshy fruits many mechanisms avoiding germination were observed (MD, MPD, PD). According to Kulhmann and Ribeiro (2016), there is a strong relationship between fruit type and dispersal syndrome in the cerrado, which is determined phylogenetically. Therefore, the diversity of dormancy classes found among zoochorous species might be related to the fact that fleshy fruits evolved many times among Angiosperms, considered thus as a labile character (Eriksson, 2016; Kulhmann and Ribero, 2016). On the other hand, fruits with autochory and anemochory are phylogenetically restricted (Kulhmann and Ribeiro, 2016). To further test this assumption germination experiments with a larger and more diverse species pool are needed.

Seed mass varied with dispersal season and dormancy class, but not with dispersal syndrome. Seeds dispersed in the dry season and in the dry-to-rainy season transition had greater seed mass than seeds dispersed in the rainy season and in the rainy-to-dry transition. Moreover, species with MPD had greater seed mass than the seeds in other dormancy classes. Only two species had MPD, *Xylopia aromatica* and *Virola sebifera*, and the largest seed in the community belonged to *V. sebifera* (7.5 times heavier than the community's mean seed mass). Thus, the difference in seed mass between dormancy classes is clearly influenced by the great seed mass of *V. sebifera*. Studies in seasonally dry environments, found seedlings of larger seeds are more likely to survive than seedlings of smaller seeds (Moles, 2018). However, seed mass is strongly affected by growth form, increasing with plant height (Moles, 2018). Therefore, the difference we detected in seed mass may be related to differences in growth form, since most species dispersing in the dry season and in the dry-to-rainy transition were trees, while species dispersing in the rainy season and in the rainy-to-dry transition also included shrubs and forbs.

In conclusion, most cerrado species germinated at the beginning of the rainy season and both dispersal season and seed dormancy controlled the timing of seed germination. The likelihood of a species being dormant depended upon the interaction between dispersal season and syndrome, where species with limited dispersal (autochory) tend to be dormant, while species with long-distant dispersal (anemochory and zoochory) tend to be dormant if dispersal occurred during the rainy-to-dry transition. Therefore, dispersal during the rainy-to-dry transition favors the evolution of seed dormancy as the environmental conditions are favorable for germination but not for seedling establishment. Avoiding germination during the dry season was a convergent character, since all species dispersing seeds during such period had dormant seeds independent of taxonomy or dispersal syndrome. On the other hand, dormancy in autochorous species may be related to distributing the risk of seedling mortality through time, which is supported by the lack of a seasonal germination pattern and a high coefficient of variation found in the mean germination time of these species. Additionally, dormancy class was related to dispersal season and syndrome, but not with seed mass and moisture contents. Aside from showing patterns of fruiting and germination phenology at a community level in cerrado, our results clarify how dormancy and dormancy classes are modulated by the interaction between dispersal season and syndrome, allowing a better understanding of the evolution of seed dormancy in seasonally dry tropical habitats such as the cerrado.

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SUPPLEMENTARY DATA

Table S1. Climate characteristics of the four different seasons in a cerrado community in southeastern Brazil.

Season	Temperature (°C)			Precipitation (mm)	Rainy days	Potencial evapotranspiration	P-ETP (mm)
	Minimal	Mean	Maximal				
Rainy	16.8±1,37	23±0.92	29.2±1,17	231.3±105.3	15.5±4.45	106.3±9.89	107±105
Rainy to dry	14.8±1,37	21.4±0,9	28,0±1.01	83.6±48.12	7.8±2.75	82.45±7.01	1.12±47,16
Dry	10.5±1.79	17.8±1.25	25.5±1.46	44.5±46.06	4.77±3.41	51.47±8.72	-6.98±45.19
Dry to rainy	13.5±1.6	20.9±1.46	28.4±1.94	92.54±59.83	8.8±3.89	80.6±14.84	11.93±60.46

P-ETP = Precipitation minus potential evapotranspiration

Table S2. Seed germination traits of 28 species used for determined the estimated germination date in a cerrado community, southeastern Brazil, ordered by dispersal syndrome, the respective ecological information: dispersal season: Rainy = rainy season (Nov to Mar); Dry = dry season (May to Aug); Rainy-dry = rainy-to-dry season transition (April); Dry-rainy = dry-to-rainy season transition (Sept to Oct); dormancy class: ND = non-dormant; PD = physiological dormancy; PY = physical dormancy; MD = morphological dormancy; MPD = morphophysiological dormancy. Total germ: total germination percentage at optimal temperature; MGT: mean germination time; SD MGT: standard deviation of the mean germination time; Germination time: the addition of MGT and SD MGT; CV MGT: coefficient variation of MGT.

Species	Dispersal syndrome	Dispersal season	Dormancy class	Total Germ (%)	MGT (days)	SD MGT (days)	Germination time (days)	CV MGT (%)
Kielmeyera coriacea	Anemochory	Dry	ND	97.4	12.41	1.52	13.93	12.27
Dalbergia misculobium	Anemochory	Dry	ND	100	6.73	0.92	7.64	13.63
Machaerium acutifolium	Anemochory	Dry	ND	60	40.8	5.50	46.3	13.48
Plathymenia reticulata	Anemochory	Dry	PY	77.5	68.02	7.76	75.78	11.4
Qualea dichotoma	Anemochory	Dry	ND	100	8.5	0.82	9.32	9.64
Qualea grandiflora	Anemochory	Dry	ND	96	13.86	1.08	14.94	7.78
Vochysia tucanorum	Anemochory	Dry	ND	90.4	15.23	0.94	16.17	6.19
Anadenanthera falcata	Autochory	Dry	ND	73.3	4.2	1.20	5.39	28.54
Chamaecrista desvauxii	Autochory	Rain-dry	PY	79.4	150.09	38.85	188.94	25.89

Dimorphandra mollis	Autochory	Dry	PY	67.5	100.9	22.94	123.84	22.73
Mimosa sommians	Autochory	Rain-dry	PY	100	24.15	13.63	37.78	56.43
Stryphnodendron obovatum	Autochory	Dry	PY	66.7	77.64	10.53	88.17	13.56
Schefflera vinosa	Zoochory	Dry	MD	82.6	30.7	1.86	32.56	6.07
Ananas ananassoides	Zoochory	Rain	MD	96.7	26.29	0.79	27.08	3.0
Erythroxylum cuneifolium	Zoochory	Rain	ND	93.8	12.01	0.87	12.89	7.28
Ocotea pulchella	Zoochory	Dry-rain	ND	80	18.96	2.36	21.32	12.47
Strychnos sp	Zoochory	Dry-rain	PD	52.6	60.35	14.16	74.51	23.47
Leandra solenifera	Zoochory	Rain	ND	85.8	19.03	1.77	20.8	9.3
Miconia albicans	Zoochory	Rain	ND	81.9	13.97	1.26	15.23	9.03
Miconia chamisois	Zoochory	Dry	ND	82.5	12.15	0.61	12.76	5.04
Miconia fallax	Zoochory	Rain	ND	61.9	13.04	3.56	16.61	27.33
Miconia ligustroides	Zoochory	Rain	ND	96.2	22.66	1.75	24.41	7.72
Miconia rubiginosa	Zoochory	Rain	ND	87.2	20.35	1.71	22.06	8.42
Myrcia guianensis	Zoochory	Rain	ND	91.1	6.52	0.64	7.16	9.87
Myrcia splendens	Zoochory	Rain	ND	100	5.13	1.14	6.27	22.28
Myrsine guianensis	Zoochory	Rain	PD	80.3	192.9	46.39	237.69	24.25
Amaioua guianensis	Zoochory	Dry	ND	91.7	31.75	3.55	35.29	11.17
Psychotria hoffmannseggiana	Zoochory	Rain-dry	PD	61.8	61.59	6.50	68.09	10.55

Table S3. Circular Statistics parameters from fruiting phenology for the community and for each dispersal syndrome in a cerrado community, southeastern Brazil.

	Community	Anemochory	Autochory	Zoochory
Number of Observations	34	7	5	22
Mean Vector (µ)	280.838°	239.215°	172.091°	7.818°
Average fruiting peak date	October 10th	August 27th	June 21th	January 7th
Length of Mean Vector (r)	0.126	0.931	0.592	0.325
Median	266.336°	228.822°	177.484°	352.18°
Concentration	0.255	4.612	1.207	0.686
Circular Variance	0.874	0.069	0.408	0.675
Circular Standard Deviation	116.558°	21.746°	58.654°	85.956°
Rayleigh Test (Z)	0.542	6.061	1.753	2.317
Rayleigh Test (p)	0.585	**2.7E-04**	0.178	0.098

The Rayleigh test p values in bold indicates the occurrence of seasonal patterns

Table S4. Circular Statistics parameters from estimated germination date for the community and for each dispersal syndrome in a cerrado community, southeastern Brazil.

	Community	Anemochory	Autochory	Zoochory
Number of Observations	28	7	5	16
Mean Vector (µ)	329.132°	317.659°	291.455°	354.095°
Average estimated germination date	November 29th	November 18th	October 22th	December 25th
Length of Mean Vector (r)	0.557	0.958	0.567	0.454
Median	319.314°	314.559°	304.356°	342.247°
Concentration	1.32	7.528	1.089	1.017
Circular Variance	0.45	0.042	0.433	0.546
Circular Standard Deviation	62.655°	16.765°	61.082°	72.012°
Rayleigh Test (Z)	8.469	6.426	1.605	3.297
Rayleigh Test (p)	**<0.001**	**<0.001**	0.209	**0.034**

The Rayleigh test p values in bold indicates the occurrence of seasonal patterns

Table S5. Summary of the factorial PERMANOVA to evaluate the effects of dormancy class, dispersal season, dispersal syndrome and their interactions on seed mass in a cerrado community in southeastern Brazil.

Source	Df	RSumSq	RMeanSq	Iterations	P
Dispersal syndrome	2	0.00427	0.002135	732	0.199
Dormancy class	4	0.07828	0.01957	5000	**0.019***
Dispersal syndrome:Dormancy class	1	0.00344	0.003445	1052	0.088
Dispersal season	3	0.04414	0.014712	3667	**0.043***
Dispersal syndrome:Dispersal season	2	0.01258	0.006288	1758	0.081
Dormancy class:Dispersal season	3	0.03612	0.01204	5000	0.088
Residuals	18	0.03262	0.00181		

The significant factors according to p values, is given in bold; d.f. = degrees of freedom

Table S6. Summary of the factorial PERMANOVA to evaluate the effects of dormancy class, dispersal season, dispersal syndrome and their interactions on seed moisture content in a cerrado community in southeastern Brazil.

Source	Df	RSumSq	RMeanSq	Iterations	P
Dispersal syndrome	2	138.56	69.28	191	0.5864
Dispersal season	3	324.83	108.28	494	0.5850
Dispersal syndrome:Dispersal season	3	443.48	147.83	419	0.4439
Dormancy class	4	1035.78	258.95	2238	0.3070
Dispersal season:Dormancy class	3	355.96	118.65	443	0.5192
Residuals	14	2552.52	182.32		

The significant factors according to p values, is given in bold; d.f. = degrees of freedom

Table S7. Standardized residues of the log linear model evaluating the relationship between dispersal syndrome, dispersal season and dormancy in a cerrado community in southeastern Brazil.

		Dispersal syndrome		
	Season	Anemochory	Autochory	Zoochory
Non dormant	Dry	0.57	-1.455	0.575
	Dry to rain	0.996	0.575	-0.416
	Rainy	0	0	0.415
	Rainy to dry	0	-1.455	-1.782
Dormant	Dry	-0.707	0.947	-0.97
	Dry to rainy	-1.68	-0.97	0.404
	Rainy	0	0	-0.467
	Rainy to dry	0	0.947	1.16

Table S8. Standardized residues of the log linear model evaluating the relationship between dispersal syndrome, dispersal season and dormancy class in a cerrado community in southeastern Brazil.

Dormancy class	Season	Dispersal syndrome Anemochory	Autochory	Zoochory
MD	Dry	0	0	-0.426
	Dry to rainy	0	0	0.697
	Rainy	0	0	-1.537
	Rainy to dry	0	0	-0.739
MPD	Dry	0	0	-0.426
	Dry to rainy	0	0	0.697
	Rainy	0	0	-1.537
	Rainy to dry	0	0	1.067
ND	Dry	-0.237	-0.894	0.622
	Dry to rainy	0.26	1.272	-0.328
	Rainy	0	0	0.568
	Rainy to dry	0	-0.894	-1.732
PD	Dry	0	0	-0.798
	Dry to rainy	0	0	-0.503
	Rainy	0	0	-0.067
	Rainy to dry	0	0	0.932
PY	Dry	0.512	0.304	0
	Dry to rainy	-0.926	-1.265	0
	Rainy	0	0	0
	Rainy to dry	0	0.304	0

CAPÍTULO 2

The adaptive value of seed dormancy in seasonally dry environments

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The adaptive value of seed dormancy in seasonally dry environments

Abstract

Seed dormancy is expected to be selected in seasonally dry environments as a mechanism that synchronizes the timing of seed germination with the favorable period for seedling establishment and that distributes seedling establishment in time, decreasing the chances of all seedlings dying due to unpredictable events. However, dispersal phenology and germination niche may also synchronize germination with the favorable period for seedling establishment, and seed dispersal can substitute dormancy in order to cope with environmental heterogeneity. Thus, we propose that the adaptative value of dormancy will depend on other life-history traits that affect the timing of seed germination and the seed dispersal capacity. Seed dormancy, dispersal syndromes (a proxy of seed dispersal capacity), seed mass, dispersal season, and germination niche were characterized for 82 Cerrado species from 26 families, including the main lineages of angiosperms and a broad spectrum of growth forms. For such, we tested the following hypotheses within a phylogenetically informed framework: (1) the joint evolution of dormancy, dispersal syndromes, seed mass, and dispersal season, (2) whether seed dormancy and germination niche are alternative mechanisms to synchronize seed germination with the favorable seedling establishment period, and whether the relative importance of this mechanism varies with dispersal season, and (3) the importance of dormancy as a risk-reduction mechanism in seasonally dry environments and their trade-off with seed dispersal. Our results show that seed dormancy is evolutionarily correlated with dispersal syndrome. Additionally, seed dormancy and germination niche are key mechanisms to synchronize early plant development with the favorable season for seedling establishment, and the relative importance of these mechanisms vary with dispersal season. A trade-off between seed dispersal and dormancy was confirmed, thus seed dormancy is crucial to spread the risk of recruitment only in species with limited dispersal capacity. In conclusion, dormancy is an adaptive trait in Cerrado as it increases the chances of seedling establishment by synchronizing seed germination with the favorable season for establishment and by spreading the risk of recruitment of species with limited dispersal capacity.

Keywords: Cerrado, Neotropical savannas, environmental heterogeneity, germination niche, dispersal phenology, risk reduction mechanisms.

Introduction

In seasonally dry environments, seed germination and seedling establishment are constraint by rainfall seasonality and spatiotemporal environmental heterogeneity (Garwood, 1983; Franco, 2002, Veenendaal et al., 1996, Marod et al., 2002, Viera et al., 2008, Salazar et al., 2012). Rainfall is concentrated to one season, limiting the time seedlings have to establish. Thus, synchronizing germination with the beginning of the rainy season will increase plant success as it maximizes the establishment period, increasing the chances of seedlings surviving the subsequent dry season (Frankie et al., 1974; Garwood, 1983; Franco, 2002; Oliveira, 2008; Escobar et al., 2018). On the other hand, unpredictable dry spells during the rainy season and a great spatial variation of resource availability can increase seedling mortality, favoring risk reduction mechanism that spread seedlings in time or space (Engelbrecht et al., 2006; Viera et al., 2008; Salazar et al., 2012; Buoro & Carlson 2014).

Seed dormancy delays germination of seeds dispersed during favorable periods for germination but not for seedling establishment, such as the end of the rainy season and beginning of the dry season, to the onset of the subsequent rainy season and is considered the main mechanism controlling the timing of seed germination in seasonally dry environments (Garwood, 1983; Probert, 2000; Jurado & Flores, 2005; Salazar et al., 2011; Baskin & Baskin, 2014; Ramos et al., 2017; Escobar et al., 2018). However, dispersal phenology and germination niche may also synchronize germination with favorable seasons for seedling establishment (Garwood, 1983; Donohue, 2005; Sautu et al., 2007; Salazar et al., 2011, Ramos et al., 2017, Escobar et al. 2018, Fernandez-Pascual et al., 2017). Since seasonal environments show a predictable variation in environmental conditions, dispersing nondormant seeds at the beginning of the germination season is a common strategy controlling the timing of seed germination in these environments (Garwood, 1983; Oliveira, 2008; Baskin & Baskin, 2014; Ramos et al., 2017; Escobar et al., 2018). Seed germination niche, defined as the range of environmental conditions in which a plant can complete a successful transition from seed to seedling (Grubb, 1977), also controls timing of germination as seeds avoid germinating during unfavorable periods for seedling establishment by having specific environmental requirements for germination (Donohue, 2005; Baskin & Baskin, 2014; Fernandez-Pascual et al., 2017).

Seed dormancy can enhance seedling establishment in seasonal environments not only by synchronizing germination with the favorable season for establishment, but also by distributing the risk of seedling mortality by increasing the variation of germination time (Jurado & Flores, 2005; Simons & Johnston, 2006; Venable, 2007; Baskin & Baskin, 2014). Distributing the germination time, and consequently seedling establishment, within or among years (i.e., temporal dispersal) is considered a risk-reduction strategy, given it decreases the chances of all seedlings dying due to unpredictable events. However, it also reduces the expected success given only some seedlings will experience favorable conditions for establishment (Simons & Johnston, 2006; Snyder, 2006; Buoro & Carlson, 2014; Rubio de Casas et al., 2015). Additionally, the risk of reproductive failure is also reduced with a larger seed spatial dispersal as the likelihood of seeds finding suitable sites for germination and seedling establishment will increase if seeds are dispersed throughout many different areas (Snyder, 2006; Buoro & Carlson, 2014).

Even though both spatial and temporal dispersal serve the same purpose, they are not equivalent and the proportion each strategy contributes to recruit new individuals will depend on environmental heterogeneity (Buoro & Carlson 2014). Thus, temporal dispersal is favored in unpredictable environments that have little spatial heterogeneity, such as deserts or arid savannas. On the other hand, spatial dispersal is favored when spatial heterogeneity is high and temporal variation of environmental conditions is low or predictable, such as seasonally dry environments (Simons and Johnston 2006, Buoro & Carlson 2014; Rubio de Casas et al., 2015). However, in seasonally dry environments, unpredictable events such as dry spells during the rainy season are important sources of seedlings mortality that increase the temporal environmental heterogeneity, and can favor temporal dispersal (Veenedaal et al., 1996; Kanegae et al., 2000; McLaren & McDonald, 2003; Engelbrecht et al., 2006).

In seasonally dry environments, the role of seed dormancy as a mechanism that synchronizes germination with the onset of the rainy season has been long recognized (Garwood, 1983; Donahue et al., 2010; Baskin & Baskin, 2014). Nevertheless, its role as a risk-reduction strategy and its interactions with spatial dispersal have been underexplored in these environments (Rubio de Casas et al., 2017). Given the trade-off between spatial and temporal dispersal, and considering that both are related to the moment in which seeds are dispersed (Ramos et al., 2017; Escobar et al., 2018), we expect a joint evolution of dispersal phenology, seed dormancy, and spatial dispersal.

Additionally, seed mass can also be evolutionary correlated with seed dormancy as larger seeds could be an alternative to dormancy in order to avoid unfavorable conditions (Venable & Brown, 1988; Rees, 1996; Rubio de Casas et al., 2017). However, studies that include a high diversity of species do not support such relationship (Jurado & Flores 2005; Norden et al., 2009; Wyse & Dickie, 2017). Therefore, the adaptative value of dormancy as a mechanism that synchronizes germination with the onset of the rainy season will depend on other life-history traits that affect the timing of seed germination, such as germination niche and dispersal season, while its value as a risk-reduction strategy will depend on spatial dispersal (Figure 1A).

(A)

Limiting factors for seedling establishment	**Plant response**	**Mechanisms used to face limiting factors**	**Relative importance of seed dormancy can be modulated by species evolutionary history and seed mass**
Rainfall seasonality	Synchronize seed germination with the onset of the rainy season	**Seed dormancy**: delay seed germination to the onset of the rainy season	
		Dispersal season: release non-dormant seeds with the onset of the rainy season	
		Germination niche: specific germination requirements avoid germination during unfavorable periods	
Spatio-temporal environmental heterogeneity	Risk reduction mechanisms	**Seed dormancy** (temporal dispersal): Increase the variation of germination time, spreading offspring within years or among years	
		Spatial dispersal: spread offspring across multiple location	

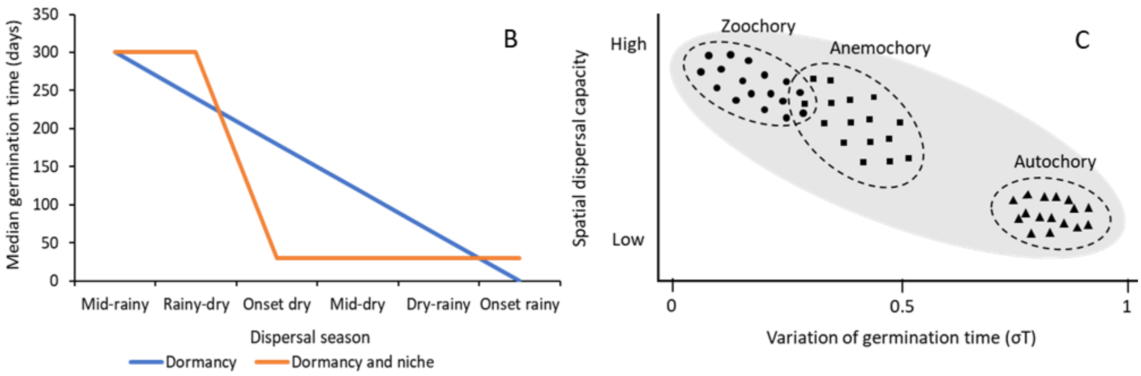

Figure 1. A) Conceptual framework showing the main limiting factors for germination and seedling establishment and the mechanisms used to overcome them in seasonally dry environments. Note that dormancy controls both aspects related to germination phenology: germination time (i.e. T50) and the temporal pattern of germination (concentrated in one event or dispersed in many events; i.e. σT). We propose that the adaptative value of dormancy as a mechanism that synchronizes germination will depend on other life-history traits that affect the timing of seed germination (germination niche and dispersal season), while its value as a risk-reduction strategy will depend on seed spatial dispersal. B) Predicted relationships between germination time and dispersal season according to the mechanism used to synchronize germination with the onset of the rainy season. If seed dormancy is the only mechanism synchronizing germination, then germination time increases as seed dispersal occurs furthest from the rainy season (blue line). However, if germination niche is also acting as a synchronizing mechanism, then we expect the germination time to decrease (orange line; in this hypothetical example, seed dormancy controls the germination time of seeds released late in the rainy season but the germination niche controls the germination time of seeds released during the dry season). C) Predicted relationship between spatial dispersal capacity and temporal dispersion. We expect that temporal dispersion (measured as the variation in germination time, σT) will be highest in species with the lowest spatial dispersal capacity (autochorous species).

To address the adaptive value of seed dormancy in seasonal environments, we used the Cerrado (Brazilian savanna) as a case study, and we hypothesize that seed dormancy is a key adaptation of plant species to these seasonally dry environments. We propose that seed dormancy plays two roles: (i) it synchronizes early plant development with the favorable season for seedling establishment and (ii) it spreads the risk of recruitment in time. In these scenarios, the evolution of dormancy is linked to other mechanisms of habitat selection, such as germination requirements, dispersal phenology, and spatial dispersal. To explore these ideas, we characterized the dormancy of 82 Cerrado species and their association to dispersal syndromes, seed mass, dispersal season, and germination requirements. Specifically, we aimed to: (1) evaluate the association between dormancy, dispersal syndromes, seed mass, and dispersal season at an evolutionary level. If seed dormancy is adaptive, dormant seeds should be more frequent than expected by chance or mere evolutionary inertia and thus exhibit a pattern of phylogenetic conservatism; (2) determine whether seed dormancy and germination niche are alternative mechanisms to synchronize seed germination with the onset of the rainy season, and whether the relative importance of this mechanism varies with dispersal season. If seed dormancy is selected to ensure the synchronization of germination, then germination time (T50) should be highest when seeds are dispersed far away from their germination season, unless these seeds require a very specific germination niche (Figure 1B); and (3) evaluate the importance of dormancy as a risk-reduction mechanism in seasonally dry environments. If seed dormancy spreads the risk of recruitment in time, it should not only entail a delay in germination but also an increase in the variation of germination time (σT, Figure 1A). Since seed spatial dispersal can play a similar role by spreading recruitment risks and costs in space instead of time, we also explored if the variation of germination time is related to dispersal syndrome (a proxy of spatial dispersal capacity). We expected that such variation of germination time should be highest in seeds that tend to disperse closer to their relatives (e.g., autochorous, Figure 1C).

Material and Methods

Study area

The study was conducted in two Cerrado savanna areas: the private *Fazenda Botelho* and the São Paulo Ecological Station *Estação Ecológica de Itirapina* located in

Itirapina, south-eastern Brazil (22° 13’ to 22° 10’S; 47° 55’ toa 47° 51’W). Both areas are at an altitude of 770 m and are separated by less than 3 km. *Fazenda Botelho* is predominately covered by typical *Cerrado strict sense* or woodland savanna (Oliveira-Filho and Ratter, 2002), characterized by a dominant woody layer (trees and shrubs ranging from 3 to 12 m in height and a crown cover of 30 to 90%) and a scattered herbaceous layer (Reys et al 2013, Camargo et al. 2018, Escobar et al. 2018). *Estação Ecológica de Itirapina* is dominated by *Cerrado campo sujo* or grassland to scrubland savanna (Oliveira-Filho and Ratter, 2002), characterized by a continuous herbaceous layer (subshrubs, herbs, but mostly graminoids) with scattered shrubs and small trees (Tannus et al. 2006, Zanchetta 2006). The climate is tropical with a wet warm season (summer) from October to March, a dry cold season (winter) from April to September, mean annual precipitation of 1513 mm, minimum mean temperatures of 9 ºC in July, maximum mean temperatures of 30 ºC in February, and a mean annual temperature of 20.8°C.

The germination in Cerrado is seasonal and is concentrated in a two-month period that coincides with the onset of the rainy season (November and December; Escobar et al. 2018). Therefore, we divided the year into six two-month seasons: **onset rainy** season - start of the rainy season (November and December), **mid-rainy** season (January and February), **rainy-dry** – the rainy to dry season transition (March and April), **onset dry** - start of the dry season (May and June), **mid-dry** season (July and August), **dry-rainy** – the dry to rainy season transition (September and October), see Fig. 2A,B. Such division is consistent with the climatic data of the study area (mean for years 1982–2012, CRHEA–EESC/USP meteorological station) and was carried out in order to estimate how far the dispersal season of a given species is from the favorable period for germination. For instance, the period furthest from the optimal germination period would be the mid-rainy season and seeds dispersed in such season are expected to wait for nearly one year before reaching favorable conditions for germination. On the other hand, the period closest to the optimal germination period would be the dry-to-rainy transition and the onset of the rainy season.

Fruit and seed collection

Fruit and seed collection, and seed storage was carried out according to the protocols described in Escobar et al. (2018). In the woodland savanna area, fruits were collected biweekly between March 2015 and March 2016; in the grassland area, fruits were collected monthly between June 2016 and June 2017. We collected 82 species belonging to 25 families: 34 species in the woodland savanna and 48 species in the grassland savanna (Supplementary Table 1).

Seed mass

To determine the seed mass of each species, 100 recently harvested seeds were weighed individually (for seeds weighing >0.001 g) or in eight groups of 100 seeds each (for seeds weighing <0.001 g) with an analytical scale (Ohaus, Pioneer PA214; Ohaus, New Jersey, USA).

Dispersal syndrome

Species dispersal syndromes were classified according to morphological characteristics of the diaspores; field observations were complemented by information extracted from the literature (Morellato and Leitão-Filho, 1992; Oliveira and Moreira, 1992; Batalha and Mantovani, 2000; Weiser and Godoy, 2001; Tannus et al., 2006; Camargo et al., 2013). According to Pérez-Harguindeguy et al. (2013), the zoochorous species had fleshy fruits or fleshy structures partially or totally involving seeds, or fruits and seeds that contain appendages (e.g. hooks, sticky substances) which become attached to animals; anemochorous species had winged or flat diaspores with a large area:volume ratio (e.g. pappus), or minute dust-like seeds (seed mass <0.1 mg for Cerrado species; Oliveira and Garcia, 2011, Pereira et al., 2014, Dugarte et al., 2015, Giorni et al., 2018); autochorous species did not show structures known to facilitate wind or animal dispersal and had a seed mass ≥ 0.1mg.

Dispersal season

Dispersal season of species was determined according to the fruiting peak date. Thus, species were classified as releasing seeds in one of the six two-month seasons previously described. For 24 out of the 82 species collected in the present study, the fruiting peak was determined based on the 11-year database (2005–15) of the Phenology Laboratory at UNESP (Escobar et al., 2018). For the remaining species, the fruiting peak was determined based on the seed collection dates, which were carried out throughout 2015, 2016, and 2017.

Seed germination experiments

We determined seed dormancy and optimal germination temperature based on germination experiments covering a wide range of temperatures (Supplementary Table 1). For the 34 species collected in the woodland savanna area, we used the germination data of Escobar et al. (2018). For the 48 grassland species, we carried out germination experiments in which seeds were placed in Petri dishes with two layers of filter paper saturated with distilled water under 24-h white light (≈32 µmol m^{-2} s^{-1}), and up to five constant temperatures and one alternating temperature (20/30 °C; Supplementary Table 1). For each species, we used five to six replicates containing 20–25 seeds for each temperature according to seed availability. Germination was determined by radicle curvature or protrusion of aerial structures (e.g. cotyledons or plumules; Northam and Callihan, 1994), except for dust-like seeds, in which germination occurred through the protrusion axis of the embryo (Dugarte et al., 2015). The experiments were monitored three times a week for one month, after which germination was monitored weekly for a maximum of 12 months or until the germination curve was stabilized (at least four weeks without germination; Sautu et al., 2006). At the end of the experiment, viability of non-germinated seeds was analyzed by means of the tetrazolium test, using 1 % solution at 30 °C for 48–72 h (ISTA, 2007).

Seed dormancy

Species were classified as dormant or non-dormant based on the results of the germination experiments and viability tests described above and on specific tests performed to determine seed permeability to water and embryo growth before germination (see Escobar et al., 2018 for details). We adopted the dormancy concept and classification system proposed by Baskin and Baskin (2014), where dormant seeds show one of the following characteristics: seeds with undifferentiated or undeveloped embryos, water-impermeable diaspores, or seeds that, when incubated under favorable environmental conditions for germination, show a mean germination time over 30 days. Non-dormant seeds have a mean germination time of less than 30 days, water-permeable seed coats, and totally developed embryos.

Optimal germination temperature, median germination time (T50) and coefficient of quartile variation of germination time (σT).

The optimal germination temperature of each species was determined by comparing survival germination curves at different temperatures using the Mantel-Haenszel test implemented in the function *survdiff* of the *survival* package in R (Therneau, 2018). Pos-hoc pairwise comparations were carried out with the *survdiff* function of the *survminer* package in R. We defined the optimal germination temperature as the temperature or set of temperatures at which the germination was greater and faster. In order to have accurate estimates, the optimal germination temperature was estimated for the species that had a percentage of germination greater than 30% in at least one of the incubation temperatures (71 species from 21 families, supplementary Table 2). For the survival analysis, we assumed the data were exact and, instead of using the data for every replicate separately, we combined the data of all replicates within each temperature (McNair et al., 2012). We used each seed as an experimental unit considering only viable seeds.

After establishing the optimal germination temperature, we used survival analysis to calculate the germination time 25, 50 and 75% of seeds under optimal conditions. When the optimal temperature included a wide range of temperatures, the data were grouped (pooled data). The germination times of 25, 50 and 75% of seed were estimated with a non-parametric test when the total germination percentage was above the corresponding germination fraction, and with a parametric test when the total germination percentage was below the corresponding germination fraction. For the non-parametric test, the germination time was estimated with the Kaplan–Meier estimator using the *survfit* function of the *survival* package in R (Therneau, 2018). For the parametric test, we fitted parametric survival regression models with different distributions (Weibull, exponential, gaussian, logistic, lognormal, and loglogistic) using the *survreg* function of the *survival* package in R (Therneau, 2018). We then selected the model with the maximum likelihood to predict the germination time of the germination fractions. The germination time of 50% of the seeds corresponds to the median germination time (T50).

As a measure of variation of germination time we used the coefficient of quartile variation of germination time (σT), as follows:

$$\sigma T = \frac{t75 - t25}{t75 + t25}$$

where t25 corresponds to the germination time of 25% of seeds and t75 to the germination time of 75% of seeds.

We used the coefficient of quartile variation because it is more robust than the variation coefficient or the standard deviation for non-normal distributions (Bonett, 2006), such as the germination time. The coefficient of quartile variation of germination varies between zero and one: zero when all seeds germinate at the same time (synchronous germination) and tending to one as germination becomes more asynchronous.

Germination niche and seasonal constraint to germination (Delta-T)

We used the temperature requirement for germination as a metric of the germination niche. Since the upper threshold temperature for germination is rarely reached under ecological conditions in our study site (i.e., temperatures are rarely too high for germination), the temperature requirement for germination for a given species was defined as the minimum temperature within the set of optimum germination temperatures. For example, if a species has optimal germination temperatures of 20 and 25^{o}C, its temperature requirement for germination will be 20^{o}C. Therefore, the temperature requirement for germination is equivalent to the minimum temperature condition in which seeds can reach their germination optimum. The difference between the temperature requirement for germination and the mean temperature during the season in which the species disperses its seeds was called Delta-T and was used to estimate the ecological distance between the germination and dispersal niches. For example, considering two species whose seeds are dispersed in January (mean climatic temperature 23.3°C), if one species requires at least 30°C to reach its germination optimum while the other requires 20°C, they will have a Delta-T of 6.7 and -3.3°C, respectively. Thus, Delta-T can vary from negative to positive values, and negative values or values close to zero indicate that environmental conditions do not restrict germination. On the other hand, as Delta-T increases, germination requirements are more difficult to reach and environmental conditions can restrict germination. The mean temperature in each dispersal period was calculated using 30 years of climatic data (1982–2012) from the *Centro de Recursos Hídricos e Estudos Ambientais* (CRHEA–EESC/USP) meteorological station, located ~ 6 km from the study sites.

Phylogenetic hypotheses

We used the *S.PhyloMaker* package in R to create a phylogenetic hypothesis of the cerrado plant communities studied based on the phylogeny of vascular plants PhytoPhylo (Qian and Jin, 2016), an updated version of the phylogeny of vascular plants proposed by Zanne et al. (2014). The PhytoPhylo phylogeny (the largest dated phylogeny of plants available to date) was based on seven gene regions and was time calibrated using fossil data, including all extant families of gymnosperms and angiosperms, and providing ages for all branches (Qian and Sandel, 2017).

For all species collected, the taxonomic information was standardized using the Plant List Database (http://www.theplantlist.org/). For the genera and species of the studied cerrado áreas that are absent from the PhytoPhylo phylogeny, we added them to their respective genera (in the case of species) and families (in the case of genera) using the Phylomatic and BLADJ approaches (Webb, Ackerly, & Kembel, 2008) implemented in the *S.PhyloMaker* package in R (Scenaio 3; Qian & Jin, 2016).

Data analysis

Phylogenetic signal indicates the extent to which closely related species tend to resemble each other (Blomberg et al. 2003). For continuous traits, such as seed mass, median germination time (T50), and coefficient of quartile variation of germination time (σT), the phylogenetic signal was estimated by Blomberg K statistics and Pagel λ, where K or λ = 0 indicates no phylogenetic signal, and K or λ = 1 indicates a high phylogenetic signal (Pagel 1999, Blomberg et al. 2003). Significance was assessed by comparing observed values of K or λ to the results obtained from 1000 permutations of tip reshuffling randomizations with the *phylosignal* function in the *PHYTOOLS* package in R (Revell, 2012). Since dispersal season is a discrete trait with many states (six), we codified dispersal season into a continuous variable by considering the time in months from when seeds are dispersed to the optimal germination period (November/December). We then estimated the phylogenetic signal using Blomberg's K and Pagel's λ with the *phylosignal* function in the package *PHYTOOLS* in R (Revell, 2012).

For dispersal syndrome, we tested the phylogenetic signal according to Bush et al. (2016). The minimum number of character state transitions, assuming a maximum parsimony (Maddison and Maddison 2000), was compared with the median state transitions of a randomized distribution (999 randomizations). An observed transition rate significantly less than the randomized median indicates that dispersal syndrome is significantly conserved. For dormancy, the phylogenetic signal was measured using the *phyloglm* function of *phylolm* package in R (Ho & Ané, 2014). The phylogenetic correlation parameter (alpha) was used as an indicator of the strength of the phylogenetic signal and we ran 1000 bootstrap replicates to obtain confidence intervals on the estimated alpha (Ives & Garland, 2010). For a simpler interpretation, alpha was transformed using a negative natural logarithm (a=-logα). Thus, a varies between -4 (no phylogenetic signal) and 4 (very strong phylogenetic signal).

Association of seed dormancy, seed mass, dispersal season and syndrome

To examine the relative importance of life history traits and of phylogeny on seed dormancy, we carried out two logistics regression for 82 Cerrado species. One logistic regression to test the relationship between seed dormancy and life-history traits without considering the phylogeny, and another regression considering the phylogeny. For the non-phylogenetic regression, we used a GLM (General Linear Model) with a binomial distribution to test whether seed dormancy is related to dispersal season, dispersal syndrome, and seed mass. We fitted the full model (Dormancy ~ dispersal season x dispersal syndrome x seed mass) and carried out a stepwise backward selection to choose the best model. For the phylogenetic regression, the full model used was: Dormancy ~ dispersal season + dispersal syndrome + seed mass | phylogeny.

We fitted the phylogenetic logistic regression described in Ives and Garland (2010) for the full and reduced (univariate and bivariate) models with the function *phyloglm* implemented in the *phylolm* package in R (Ho & Ané, 2014). We chose the models that had the lowest Akaike information criterion (AIC). Since seed mass was not related to dormancy nor was it conserved, we did not include it in the seasonal synchronization and risk-reduction strategy analyses.

Dormancy and seasonal synchronization

Bayesian phylogenetic multilevel models were implemented with the *brms* package (Bürkner, 2017). This approach accounts for non-independence among species by modelling species as grouping factors and adjusting the model to incorporate the covariation among species (Bürkner, 2017). To test whether the median germination time (T50) depends on seed dormancy and dispersal season, we used a Bayesian phylogenetic multilevel model with a lognormal distribution, identity link function, and the following MCMC parameters: four chains with 6000 iterations each, a burn-in period of 3000, and thinning interval = 1. The full model used was: T50 ~ Dispersal season x Dormancy + (1 | species). We used a lognormal distribution with identity link for the median germination time (T50) since the lognormal distribution had the lowest Kfold information criterion (K-fold cross-validation) in comparison to the gamma and the exponential distribution. Kfold information criterion was calculated using k=10 in the *brms* package in R (Bürkner, 2017).

The relationship between Delta-T, seed dormancy, and dispersal season was also examined with the Bayesian phylogenetic multilevel model. In this case, we used a Gaussian distribution, the identity link function, and the same MCMC parameters described above. The full model fitted was: Delta-T ~ Dormancy x Dispersal season + (1 | species). We then selected the most explanatory models comparing the full models to univariate and additive (reduced) models; we chose the model that had the lowest Kfold information criterion, using k=10 in the *brms* package in R (Bürkner, 2017).

Dormancy as a risk-reduction strategy

We tested the relationship between the coefficient of quartile variation of germination time (σT) and dormancy, dispersal season, and dispersal syndrome with a Bayesian phylogenetic multilevel model with a Gaussian distribution, the identity link function, and the same MCMC parameterization as above. The full model was: σT ~ Dormancy x Dispersal season x Dispersal syndrome + (1 | species). We contrasted the full and reduced models and chose the models that had the lowest leave-one-out cross-validation information criterion (LOOIC) using the *brms* package in R (Bürkner, 2017). Then, we compared the models with the lowest LOOIC using the Kfold with k=10 (Bürkner, 2017).

Results

In this study, we examined seeds from 82 species and 26 families, including forbs and grasses, subshrubs, shrubs, and trees (Supplementary Table S1). The proportion of dormant species was slightly lower than that of non-dormant (44 and 56 %, respectively). Dispersal syndromes were also equally represented, both zoochory and anemochory were present in 35.1% of species and autochory in 29.9% (Supplementary Table S1). Seed dispersal occurred throughout the year, but most seeds were dispersed between the onset of the rainy season and the rainy-to-dry season transition (Fig. 2A). Seed dormancy showed a seasonal pattern: it was highest between the mid-rainy and the onset of the dry season (53-67% of dormant species) but gradually decreased until the onset of the rainy season (only 14.3% of dormant species, Fig. 2A). Dispersal phenology differed according to dispersal syndromes (chi2=25.392, p=0.004, iterations=10000, Supplementary Table S3, Fig. 2B). Thus, seed dispersal of anemochorous species was concentrated between the mid-dry season and the onset of the rainy season (July to December); autochorous species dispersed seeds mainly from mid-rainy season to the onset of the dry season (January to June); while for zoochorous species, seed dispersal occurred throughout the year but was lowest during the dry season (May to August, Fig. 2B). Few anemochorous species were dormant (17%), while nearly half of zoochorous speciess were dormant (48%) and most autochorous species were dormant (71%; Figure 2C). Seed mass varied more than four orders of magnitude, however 80% of seeds weighing between 0.001 and 0.1 g and the weight of dormant and non-dormant seeds overlapped (Fig. 2D).

The GLM model (dormancy ~dispersal syndrome + dispersal season), which was chosen after a stepwise selection, indicated that seed dormancy was related to both dispersal syndrome and season, but not to seed mass (Supplementary Table S4). The GLM model showed that seeds of autochorous and zoochorous species had a higher probability of being dormant than seeds from anemochorous species, and that seeds released during the dry-to-rainy transition and at the onset of the rainy season are less likely of being dormant than seeds released in other seasons (Supplementary Table S4, Figure 2 A, C). However, the phylogenetic logistic regression showed that dormancy was only unambiguously related to dispersal syndrome (Table 1). Model comparisons pointed that the best fit was a reduced model: Dormancy ~ Dispersal syndrome | phylogeny, (Supplementary Table S5). This model indicated that seeds from autochorous and zoochorous species are more likely of being dormant compared to anemochorous species (phyloglm: z= 3.609, p<0.0001, and z= 2.061, p=0.039, respectively, Figure 3C), and that there is no significant difference between autochorous and zoochorous species (phyloglm: z= -1.584, p=0.113). Seed dormancy presented a high degree of phylogenetic correlation (a=1.2, p<0.01) and conservatism, as did dispersal syndrome (p<0.01) and the median germination time (K=0.197, p=0.033; Lambda=0.848, p=0.001), while seed mass (K=0.091, p=0.52; Lambda=0.256, p=0.17), dispersal season (K=0.039, p=0.99; Lambda=0.166, p=0.14), and the coefficient of quartile variation of germination time did not (K=0.087, p=0.251; Lambda=0.273, p=0.086).

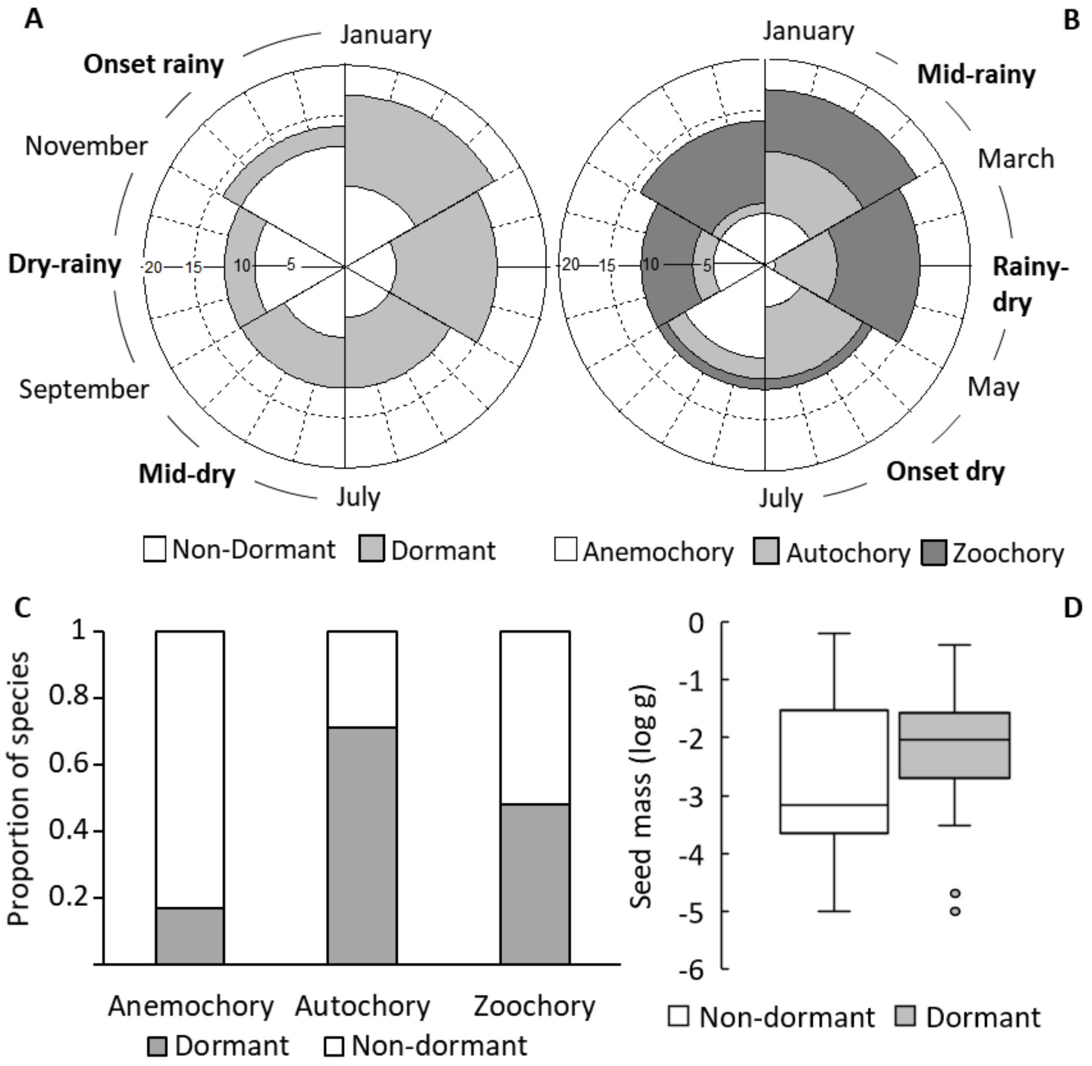

Fig. 2. Dispersal season, seed dormancy, and seed mass for 82 cerrado species, Southeastern Brazil. Number of species fruiting by dispersal season according to (A) seed dormancy and (B) dispersal syndrome. Relationship between seed dormancy and dispersal syndrome (C), and between seed dormancy and seed mass (D). Seed mass (g) was transformed by log10(g).

Table 1. Results for the phylogenetic logistic regression to evaluate the effect of seed functional traits and phylogeny on seed dormancy of cerrado species; full model: Dormancy ~ dispersal season + dispersal syndrome + seed mass | phylogeny, where seed dormancy was considered a binary variable (0 = non-dormant; 1 = dormant).

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.9106	0.84369	-2.2646	0.023*
Autochory	1.8716	0.66689	2.8064	0.005**
Zoochory	1.8266	0.74878	2.4394	0.015*
Dry-to-rainy	-0.4806	0.87367	-0.5500	0.582
Mid-dry	1.3199	0.98378	1.3417	0.18
Onset dry	1.3051	0.88832	1.4692	0.142
Rainy-to-dry	0.7894	0.76892	1.0267	0.305
Mid-rainy	0.6081	0.77081	0.7889	0.43
Seed mass	0.0052	2.03643	0.0025	0.999

Dispersal syndrome: anemochory, autochory, zoochory; dispersal seasons: onset rainy=November/December, mid-rainy=January/February, rainy-to-dry season transition =March/April, onset dry=May/June, mid-dry=July/August, dry-to-rainy season transition= September/October, onset rainy= November/December); and, seed mass. Degree of phylogenetic correlation data (a=1.5). Reference levels: anemochory and onset of the rainy season.

Dormancy and seasonal synchronization

The contrast between full and reduced models indicated that the differences in germination time are well explained by seed dormancy alone: T50 ~ Dormancy | Phylogeny (Supplementary Table S7). This means that a great proportion of the germination time data can be predicted by dormancy and by the species evolutionary history (Lynch's phylogenetic heritability=0.42, 95% CI=0;0.96). Additionally, dispersal season does not increase the explanatory power of the model as indicated by the deviance value (sigma). However, the interaction between seed dormancy and dispersal season was significant (Table 2) and may explain the lower germination time found during the onset of dry season (Fig. 3A), a season in which a high proportion of dormant species disperse their seeds (>50 %). According to the model (T50 ~ Dispersal season * Dormancy | Phylogeny), germination time was dependent on seed dormancy and on the interaction between seed dormancy and dispersal season (Table 2). Thus, the germination time of non-dormant species was short in all dispersal seasons (< 30 days), while dormant species showed a longer and more variable germination time, depending on when they dispersed their seeds (Fig 3A). The germination time of dormant seeds was shortest in species dispersing seeds with the onset of the dry season in comparison to other seasons (Figure 3A, Supplementary data Table S6). When looking at a one-year time-scale, the germination time of dormant species seems to follow a V pattern: greater germination times for seeds dispersed during the mid-rainy season and the rainy-to-dry season transition, lower germination times for seeds dispersed following the onset of the dry season, but greater germination times again after the onset of the dry season (Fig. 3A). However, even though the germination time of dormant species increased after the onset of the dry season, this has relatively small community-level effects given that less than 40% of species released seeds after the onset of the dry season are dormant and that this proportion decreases as the rainy season approaches (Fig. 2A). The seasonal pattern of germination times at the community level must be described accounting for germination time but also for the proportion of dormant species dispersing seeds at any given time. When considering these two factors simultaneously, the pattern is different: greater germination times predominate between the mid-rainy season and the rainy-to-dry season transition, then decrease abruptly with the onset of the dry season and remain constantly lower until the beginning of the subsequent rainy season (Fig. 3B).

Table 2. Results of the Bayesian phylogenetic multilevel model considering the relationship between median germination time (T50), dispersal season, dormancy, and phylogeny.

Group-Level: Species	Estimate	Est.Error	95% CI	Eff. Sample	Rhat
Sd (Intercept)	0.39	0.21	(0.02, 0.72)	235	1.02
Population-Level Effects					
Intercept	2.44	0.20	(2.04, 2.83)	3657	1.00
Dry-to-rainy	-0.03	0.30	(-0.62, 0.55)	4019	1.00
Mid-dry	-0.29	0.34	(-0.95, 0.38)	5001	1.00
Onset dry	0.20	0.36	(-0.5, 0.91)	4636	1.00
Rainy-to-dry	-0.06	0.36	(-0.77, 0.64)	4483	1.00
Mid-rainy	-0.50	0.31	(-1.12, 0.11)	4280	1.00
Dormancy	**2.16**	**0.53**	**(1.11, 3.2)**	2710	1.00
Dry-to-rainy: Dormancy	-0.19	0.69	(-1.56, 1.16)	3291	1.00
Mid-dry: Dormancy	0.27	0.72	(-1.15, 1.68)	3464	1.00
Onset dry: Dormancy	**-1.22**	**0.67**	**(-2.53, 0.01)**	2964	1.00
Rainy-to-dry: Dormancy	-0.26	0.68	(-1.58, 1.06)	3002	1.00
Mid-rain: Dormancy	0.58	0.65	(-0.68, 1.85)	2930	1.00
Sigma	0.49	0.18	(0.14, 0.76)	170	1.02

Lynch's phylogenetic heritability = 0.42, 95% CI = 0;0.96. Dispersal seasons: onset rainy=November/December, mid-rainy=January/February, rainy-to-dry season transition =March/April, onset dry=May/June, mid-dry=July/August, dry-to-rainy season transition= September/October, onset rainy= November/December. Dormancy1= dormant species. Reference levels: onset of the rainy season and non-dormancy.

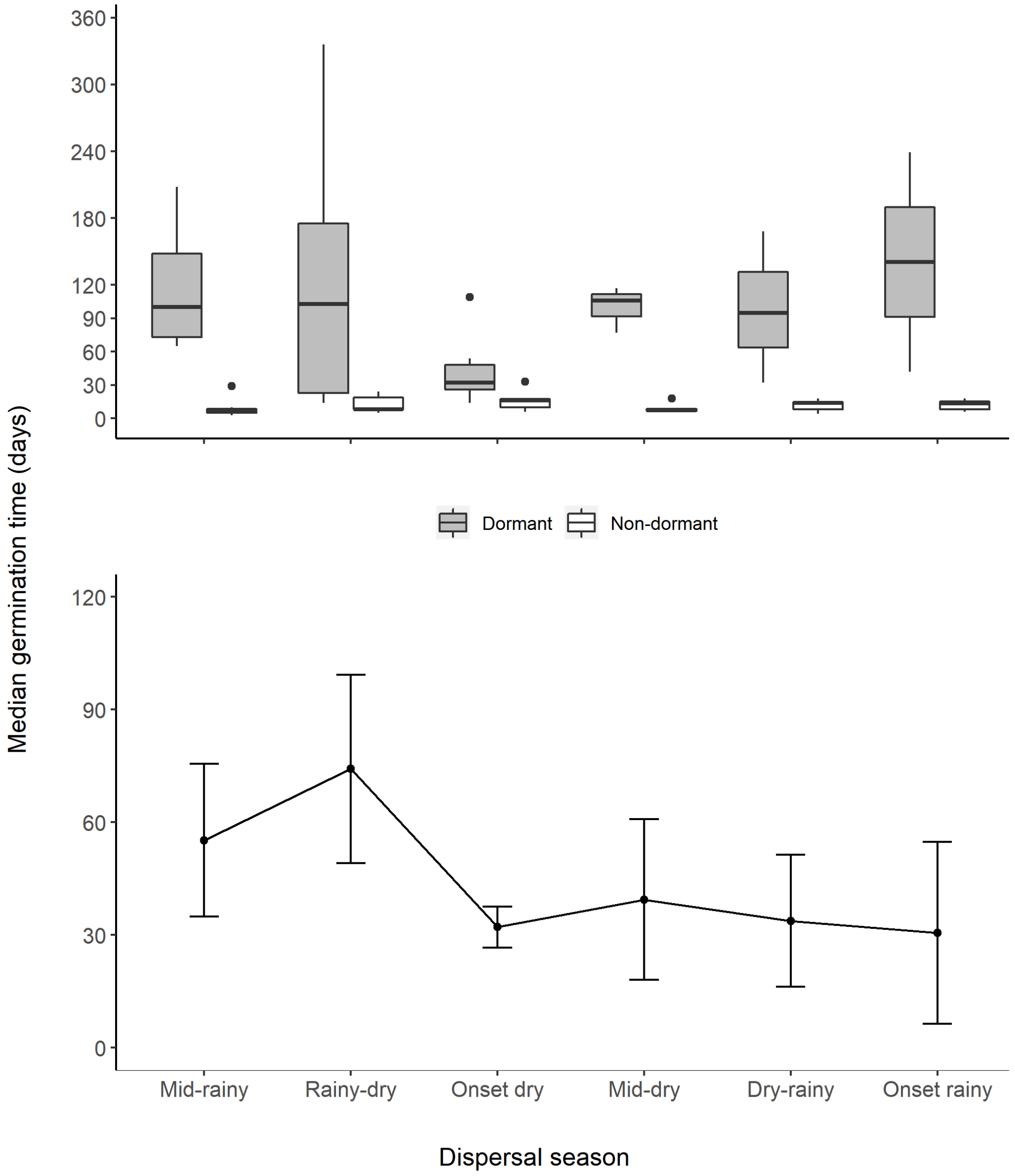

Figure 3. Median germination time (T50) for dormant (grey) and non-dormant (white) species in each dispersal season (A) and median germination time weighted for the proportion of dormant species in each dispersal season (B). The optimal germination period is the onset rainy season. Box plots show the median, the inter-quartile range of median germination time for dormant and non-dormant species across seasons. Dispersal seasons: onset rainy=November/December, mid-rainy=January/February, rainy-to-dry season transition =March/April, onset dry=May/June, mid-dry=July/August, dry-to-rainy season transition= September/October, onset rainy= November/December.

We tested if the germination niche might also contribute to synchronize germination to the optimal recruitment season. Delta-T (the difference between temperature conditions at the time of seed dispersal and temperature requirements for germination) varied with dispersal season, but not with dormancy nor with the interaction between dormancy and dispersal season (Table 3). Species dispersing seeds during the dry season showed the highest Delta-T values, regardless of dormancy. (Fig. 4A, Supplementary Table 7 and Supplementary Fig S1).

Table 3. Results of the Bayesian phylogenetic multilevel model testing if Delta-T depends on seed dormancy and dispersal season. Shifts in the germination niche relative to the ecological conditions experienced by seeds immediately after dispersal was approximated as the difference between the optimal temperature for germination and the mean temperature at the time of dispersal (Delta-T; see text for details).

Group-Level: Species	Estimate	Est.Error	95%CI	Eff.Sample	Rhat
Sd (Intercept)	2.65	1.36	(0.15, 4.72)	90	1.01
Population-Level Effects					
Intercept	2.35	1.22	(-0.07, 4.75)	3551	1.00
Dormancy	2.42	3.24	(-3.83, 8.86)	2698	1.00
Dry-to-rainy	0.63	1.86	(-2.99, 4.27)	4010	1.00
Mid-dry	**6.48**	**2.13**	**(2.30, 10.74)**	3230	1.00
Onset dry	**4.88**	**2.29**	**(0.40, 9.39)**	4296	1.00
Rainy-to-dry	2.47	2.32	(-2.05, 6.96)	3968	1.00
Mid-rain	1.87	1.92	(-1.82, 5.69)	3873	1.00
Dry-to-rainy:Dormancy	0.32	4.32	(-8.18, 8.92)	2918	1.00
Mid-dry:Dormancy	-2.49	4.45	(-11.4, 6.16)	3233	1.00
Onset dry:Dormancy	-0.25	4.09	(-8.39, 7.88)	2914	1.00
Rainy-to-dry:Dormancy	-0.42	4.21	(-8.58, 8)	2935	1.00
Mid-rain:Dormancy	-1.56	3.96	(-9.33, 6.26)	3004	1.00
Family Specific Parameters					
Sigma	2.69	1.38	(0.16, 4.68)	51	1.03

Lynch's phylogenetic heritability = 0.49, 95%CI = 0;1. Dispersal seasons: onset rainy=November/December, mid-rainy=January/February, rainy-to-dry season transition =March/April, onset dry=May/June, mid-dry=July/August, dry-to-rainy season transition= September/October, onset rainy= November/December. Dormancy= dormant species.
Reference levels: onset of the rainy season and non-dormant species.

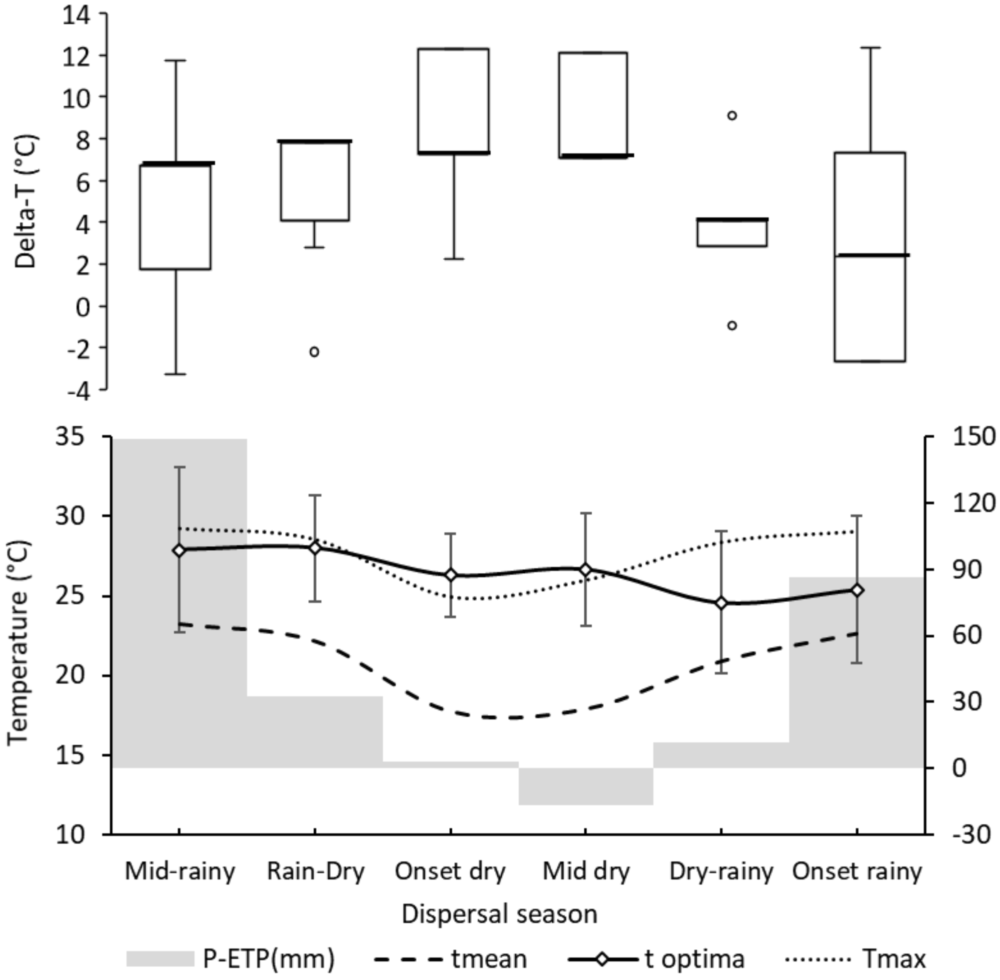

Figure 4. Relationship between dispersal season and Delta-T (difference between the minimum optimal temperature for germination and the mean temperature at the time of dispersal) for Cerrado species from Southeastern Brazil. (A) Box plot show the median, the inter-quartile range of Delta-T according to dispersal season, and B) Climatic conditions and minimum optimal temperature for germination throughout the dispersal seasons for the Cerrado study areas at Itirapina, southeastern Brazil. Minimum optimal temperature for germination (solid line) and standard deviation (vertical lines); and the mean temperatures (dashed line), maximum temperatures (dotted line), and water balance (precipitation minus potential evapotranspiration; gray bars) for a period of 30 years (1982–2012). Source for the climatic data: CRHEA–EESC/USP meteorological station.

Dormancy as a risk-reduction strategy

Univariate models showed that the variation of germination time (σT) was associated to dispersal syndrome, dispersal season, and dormancy. Thus, σT was highest in species dispersing seeds with the onset of the dry season, autochorous species or dormant species (Fig. 5; Supplementary tables 7 - 9). According to K-fold and Bayesian R^2 values, three models had similar fits to the data: one model where σT depended only on dormancy, an additive model that considered dormancy and dispersal syndrome, and a full factorial model that also considered the interaction between dormancy and dispersal syndrome (Supplementary Table S10). This means that the variation of germination time is mainly explained by dormancy, and that adding dispersal syndrome only slightly increased the fit of the model. Since σT differed significantly between dormancy states and among dispersal syndromes, but not with the interaction between the two factors (Supplementary Table S11), we chose the model σT ~ Dormancy + Dispersal syndrome. According to this model, dormant species showed a higher σT than non-dormant species regardless of dispersal syndrome, and zoochorous species showed a lower σT in comparison to autochorous species regardless of dormancy state (Fig. 5B; Table 4). Therefore, the difference of σT between autochory and anemochory is due to the proportion of dormant species within each dispersal syndrome. On the other hand, the difference between autochorous and zoochorous species was related to an overall lowest value of σT in zoochorous species, including both dormant and non-dormant zoochorous species (Fig. 5B).

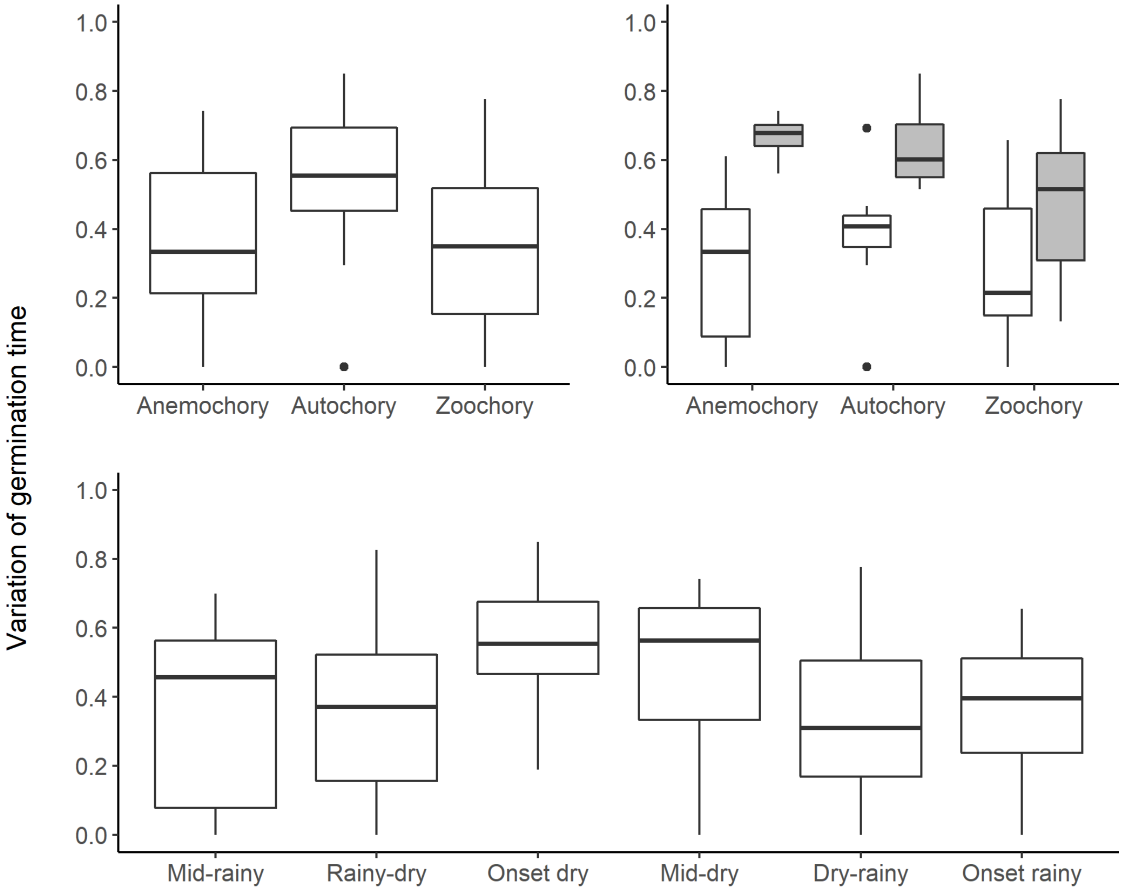

Figure 5. Variation in germination time (σT) of Cerrado species as a function of dispersal syndrome (A), dormant and non-dormant species for each dispersal syndrome (B), and dispersal season (C).

Table 4. Results of the Bayesian phylogenetic multilevel model testing if the variation in germination time (σT) depends on seed dormancy and dispersal syndrome.

Group-Level: Species	Estimate	Est.Error	95%CI	Eff.Sample	Rhat
sd(Intercept)	0.13	0.06	(0.01, 0.22)	286	1.02
Population-Level Effects					
Intercept	0.31	0.04	(0.23, 0.39)	3949	1.00
Anemochory	-0.07	0.07	(-0.21, 0.06)	2624	1.00
Zoochory	**-0.13**	**0.06**	**(-0.26, -0.01)**	2137	1.00
Dormancy	**0.26**	**0.06**	**(0.15, 0.37)**	4830	1.00
Family Specific Parameters					
Sigma	0.26	0.06	(0.15, 0.37)	413	1.01

Lynch's phylogenetic heritability = 0.49, 95%CI = 0 - 0.98. Variation in germination time did not differ between zoochorous and anemochorous species; Hypothesis test: zoochory ≠ anemochory; Estimate = -0.06, Estimate error=0.06, Confidence interval= -0.18 to 0.06. Reference levels: autochory and non-dormant species.

Discussion

Our results show that dormancy is more frequent than expected by chance in the cerrado, supporting its adaptive value. Seed dormancy co-varies with spatial dispersal, but not with dispersal season or seed mass, which points to the correlated evolution of dispersal in time and space. Seed dormancy and germination niche are key mechanisms to synchronize early plant development with the favorable season for seedling establishment, and the relative importance of these mechanisms vary with dispersal season. Moreover, in species where seed dispersal is limited to shorter distances (autochory), seed dormancy contributes to spread the risk of recruitment in time. Even though germination time (T50) and variation in germination time (σT) depend mainly on seed dormancy, these are modulated by dispersal season and spatial dispersal capacity. Therefore, we suggest that the role of dormancy varies with dispersal season and spatial dispersal capacity of seeds: dormancy may increase the germination time of seeds dispersed during the mid-rainy season and rainy-to-dry season transition in order to synchronize germination with the onset of the rainy season, and it may also increase the variation of germination time in seeds with shorter spatial dispersal so that seeds are able to cope with the dry spells that occur during the rainy season.

The evolutionary ecology of seed dormancy in the Cerrado

In cerrado, seed dormancy is contingent on the phylogenetic history and on its evolutionary and functional relation with dispersal syndrome. Although dispersal season does not determine whether a seed is dormant or not, it does control the germination time of dormant seeds. Given its labile characteristic, dispersal phenology is not intimately related to other traits, but it modulates their adaptative value, especially dormancy since it directly affects the timing of seed germination. In seasonal environments, dispersal phenology does not seem to be significantly constrained by phylogeny (Silva et al. 2011, Rubio de Casas et al. 2017, Kuhlmann and Ribeiro 2016, Cortés-Flores et al 2019). That may be explained by the strong influence of seasonality on dispersal phenology and on the different phenological strategies found within a plant community as it varies with growth forms and dispersal syndrome (Griz and Machado 2001; Oliveira 2008, Jara-Guerrero et al. 2011; Silva et al. 2011, Cortés-Flores et al. 2013, 2019). Additionally, shifts in dispersal phenology are more likely to occur than changes in certain morphological and physiological seed traits that are related to spatial dispersal and dormancy (e.g. fruits with fleshy structures, embryo size, permeability of the seed coat, etc.). This is supported by the low number of evolutionary transitions between dormancy and non-dormancy (Willis et al. 2014) and by the high values of phylogenetic signals found for morphological characteristics of fruits and dispersal syndromes (Kuhlmann and Ribeiro 2016).

Although seed mass is widely used in studies addressing plant community assembly, it may be a poor predictor of community processes and its importance most likely varies across groups of species and environments (Hallett, Standish & Hobbs 2011, Larson et al. 2016). Our results show that seed mass does not vary with dormancy and is not phylogenetically conserved, consistent with other seasonal environments (Singh et al. 2017, Barak et al. 2018, Yi et al. 2019) and with Jurado and Flores’ (2005) global review on dormancy. The values of seed mass observed in cerrado species were low (80% of seeds weigh between 0.001 and 0.1g), which may be related to the dominance, in seasonal environments, of species with desiccation-tolerant seeds (Murdoch and Ellis 2000, Tweddle et al. 2003, Pritchard et al. 2004, Escobar et al. 2018) in which seed mass is >10 times lower than desiccation-sensitive seeds (Dickie and Pritchard 2002, Daws et al. 2005, 2006, Singh et al. 2017).

However, the lability of seed mass and its inability to predict dormancy may also indicate that there are several combinations between dormancy and seed size in cerrado species, revealing the different strategies to face environmental heterogeneity (Venable & Brown 1988, Rees 1996, Rees & Westoby 1997, Volis & Bohrer 2013, Moles et al. 2018). Dispersal syndromes reflect different life history strategies because it predicts dispersal distance, seed dormancy, dispersal phenology, and seed size (Leishman et al.

2000, Oliveria 2008, Thomson et al. 2011, Tamme et al. 2014, Eriksson 2016, Ramos et al. 2017, Escobar 2018), but also because the correlation among seed traits vary with dispersal syndrome. In fact, our results confirm that dispersal syndromes may be considered as strategies, in which seed size and dormancy vary consistently: anemochorous species show light seeds (0.019±0.008g), long-distance dispersal (Thompson et al. 2011), and a low probability of having dormant seeds; autochorous species show heavy seeds (0.026±0.01g), short-distance dispersal, and a high probability of having dormant seeds; and, finally, zoochorous species show heavy seeds (0.057±0.025g), long-distance dispersal (Thompson et al. 2011), and a high probability of having dormant seeds.

Dormancy and the germination niche as synchronization mechanisms

Dispersal of non-dormant species year-round and short germination times even during the dry season indicated that seed dormancy might not be the only mechanism synchronizing germination to the onset of the rainy season among cerrado species. Our results support shifts in germination niche as a synchronization mechanism regardless of seed dormancy. Moreover, when comparing the climatic conditions (rainfall and temperature) during the last 30 years to the temperature requirements for seed germination, we observed that the germination niche would not constrain germination of species dispersing seeds during the rainy season but would constrain germination of species dispersing seeds during the dry season (Fig. 4B).

Thirty-two percent of the cerrado species dispersed seeds during the dry to rainy season transition and at the onset of the rainy season, indicating that almost one third of species synchronize dispersal phenology with the moment where environmental conditions are favorable for seedling establishment and growth. The remaining species synchronized germination with the onset of the subsequent rainy season via seed dormancy or restraints related to the germination niche. However, the importance of each mechanism varies with dispersal season: in seeds dispersed when conditions are favorable for germination but inadequate for seedling establishment, such as the mid-rainy and rainy-to-dry seasons, dormancy controls germination time; in seeds dispersed during the dry season, the difference between thermal germination niche and environmental temperatures (e.g. Delta-T) is large enough to avoid germination during the dry season; finally, in seeds dispersed during the dry-to-rainy transition, thermal requirements would not limit germination yet water availability in the soil would. Therefore, we suggest that germination niche requirements is the mechanism controlling the timing of seed germination in species whose seeds are dispersed at the beginning of the dry season, regardless of dormancy (dormant species dispersed during the dry season usually germinate in 30 to 50 days; low T50). Hence, the role of dormancy at the beginning of the dry season shifts from delaying germination (increase T50) to increasing the variation of germination time (increasing σT). This also indicates that seed germination is only possible with the increase in temperature at the beginning of the rainy season.

Even though germinating with the onset of the rainy season is largely favored in seasonal environments (Garwood 1983, Marod et al. 2002, Salazar et al. 2011, Escobar et al. 2018) and most species dispersing seeds during the mid-rainy season are dormant, it is likely that some non-dormant species, whose seeds are dispersed during the mid-rainy season, will germinate and rapidly establish as germination requirements (water balance and temperatures) are met. This most likely occurs for herbaceous and sub-shrub species that depend on the beginning of the rainy season to flower and fruit as they lose their aboveground biomass during the dry season (Batalha and Mantovani 2000, Munhoz and Felfili 2007, Ramos et al. 2014). However, germination of non-dormant species whose seeds are dispersed in the rainy-to-dry transition is expected to be inhibited by water requirements given the short period for seedling establishment (less than 2 months), the low and highly variable rainfall, and the fact that thermal requirements do not seem to limit germination.

Considering that both Delta-T and the relation between germination time and dormancy vary with dispersal season, we suggest three mechanisms of synchronizing germination with the onset of the rainy season: 1) disperse non-dormant seeds during the dry-to-rainy season transition and onset of the rainy season that will germinate promptly as they show low values of T50 and Delta-T; 2) release seeds during the mid-rainy season and rainy-to-dry season transition, delaying germination through seed dormancy (high T50); and 3) disperse seeds with the onset of the dry season and mid-dry season, where germination is avoided as germination niche requirements are not met (high values of Delta-T).

Risk-reduction strategies: seed dormancy and autochory are linked to increased variability in germination time

Our results indicated that spatial dispersal is favored over temporal dispersal as most of our species (70%) showed long-distance dispersal, similar to what was observed by Gottsberger and Silberbauer-Gottsberger (2006) and Kuhlmann and Ribeiro (2016). Additionally, spatial and temporal dispersal are negatively correlated, where species with long-distance dispersal (anemochorous and zoochorous) show a lower variation in germination time (σT) than species with short-distance dispersal (autochorous). The prevalence of spatial dispersal as a risk reduction mechanism in cerrado is expected by since the climatic variation is predictable and there is great spatial heterogeneity (Buoro & Carlson 2014, Rubio de Casas et al. 2015), both in quality and quantity of sites for seedling establishment (Franco 2002, Salazar et al., 2012). However, temporal dispersal is crucial for autochorous species as it decreases the chances of seedling mortality due to unpredictable dry spells during the rainy season.

Life-history traits suggest that anemochorous and zoochorous species respond to the great variation of microsites available for seedling establishment in different ways. Anemochorous species produce a high number of lightweight seeds (Camargo 2008) with a long reproductive window (Beckman et al. 2018), wide spatial dispersal (Thompson et al. 2011), and fast and homogenous germination, which enables the colonization of suitable microsites and reduces the risk of local extinction by maintaining connectivity between populations (Bohonak & Jenkins 2003, Buoro & Carlson 2014). Zoochorous species produce a smaller number of seeds in a shorter reproductive window (Camargo 2008, Beckman et al. 2018). Furthermore, seeds of zoochorous species are heavier and dispersal is not as random since animals tend to occupy specific habitats in a more predictable manner than abiotic dispersal vectors (Wenny 2001, Graham 2001, Spiegel and Nathan 2012). Thus, seeds of zoochorous species avoid microsites with low water availability by increasing the chances of arriving at sites favorable for establishment and survival (directed-dispersal hypothesis *sensu* Wenny 2001). The directed-dispersal hypothesis explains the low variation of germination time and may also be related to the increase in seed size of zoochorous species given it enhances density-dependent mortality (Spiegel & Nathan 2012), favoring large-seeded species whose seedlings have greater chances of surviving in comparison to seedlings originated from small seeds (Kitajina and Fenner 2000, Leishman et al. 2000, Moles &Westoby 2004, Levin et al. 2003).

Temporal dispersal is considered a strategy that allows recolonization of disturbed habitats and that reduces the risk of extinction of local populations as it spreads individuals throughout different cohorts (Bohonak & Jenkins 2003, Buoro & Carlson 2014). However, these will depend on persistent seed banks, an uncommon feature of tropical seasonal environments such as the cerrado (Salazar et al. 2011, Aires et al. 2013, Andrade and Miranda 2014, Escobar and Cardoso 2015, Ramos et al. 2017). Hence, in cerrado, temporal dispersal could be viewed as an adaptation that enables the establishment and local maintenance of autochorous species even in “low quality” microsites, such as those subject to fluctuating water availability in upper soil layers during the rainy season. In addition to a high temporal dispersal, autochorous species also show large seeds, increasing the chances of seedling survival under unfavorable conditions (Kitajina and Fenner 2000, Leishman et al. 2000). This could explain the prevalence of autochorous species in grassland Cerrado areas, in which dry spells have a greater impact on soil water deficits in upper soil layers (Batalha & Mantovani 2000, Kanegae, Braz & Franco 2000, Gottsberger & Silberbauer-Gottsberger 2006, Kuhlmann & Ribeiro 2016).

Conclusions

We have demonstrated that dormancy is an adaptive trait in cerrado species as it increases the chances of seedling establishment by synchronizing early plant development with the favorable season and by spreading the risk of recruitment of autochorous species during the rainy season. However, dormancy as a mechanism of synchronizing germination with the onset of the rainy season is limited to species dispersing seeds during the mid-rainy and rainy-to-dry season transition since, during the dry season, germination is inhibited due to restraints in germination niche requirements and, during the dry-to-rainy transition and onset of the rainy season, seed dispersal coincides with favorable environmental conditions for seedling establishment. Our results confirm a joint evolution of seed dormancy and seed dispersal, however, the role of dormancy in seasonal environments (where variation of environmental conditions is predictable) differs from temporally unpredictable environments, in which dormancy distributes the risk of seedling mortality throughout the years (Ellner & Shmida 1981, Venable and Brown 1988, Volis & Bohrer 2013, Rubio de Casas et al. 2015). Our results show that in seasonal environments, dormancy is important as it distributes the germination of autochorous species during the rainy season, thus avoiding a reproductive failure caused by unpredictable dry spells. Cerrado plant species can also cope with the interannual environmental variation by means of life-history traits, such as long-lived adults (less than 8%of Cerrado species are annuals), iteroparity, resprouting, and clonal reproduction (Oliveira-Filho and Ratter 2002, Batalha and Martins 2002, Simon et al. 2009), which appears as alternatives of dormancy as a risk-spreading strategy across years (Rees 1996).

Finally, dormancy is key to understand the great plant diversity of cerrado, not only because it increases the chances of seedling establishment, but also because it is crucial for the recruitment of autochorous species in different sites that would otherwise be unfavorable for the establishment of anemochorous and zoochorous species, contributing to the coexistence of species with different strategies to cope with the great spatial heterogeneity for establishment.

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Supplementary data

Table S1. List of species sampled for the germination tests at two Cerrado savanna areas: the private Fazenda Botelho and the São Paulo Ecological Station Estação Ecológica de Itirapina located in Itirapina, south-eastern Brazil (22° 13' to 22° 10'S; 47° 55' to 47° 51'W). List ordered by family and species name, and the respective ecological and experimental information: cerrado physiognomy of seed collection, fruiting peak date (see Materials and methods section for calculations), growth form (tree, shrub, subshrub and herb), dispersal syndrome (zoochory, anemochory, autochory), dispersal season (onset rainy= November to December; Mid-rainy= January to February; rainy-dry transition= March to April; onset dry = May to June; Mid-dry = July to August; dry-rainy transition = September to October). Dormancy (ND = non-dormant; D = Dormant). Temperatures of the germination experiments, which were set up according to seed availability and germination percentage in optimal germination temperature (%G).

Family	Species	Physiognomy	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)	%G
Annonaceae	*Xylopia aromatica*	Woodland	April	Tree	Zoochory	D	Rainy-dry	25	0.0
Araliaceae	*Schefflera vinosa*	Woodland	September	Shrub	Zoochory	D	Dry-rainy	15; 20; 25; 30; 35	82.6
Asteraceae	*Chromolaena squalida*	Grassland	June	Subshrub	Anemochory	ND	Onset dry	15;20;25;30;35;20/30	84.9
Asteraceae	*Vernonanthura* sp.	Grassland	July	Subshrub	Anemochory	D	Mid-dry	20;25;30;20/30	46.9
Asteraceae	*Elephantopus biflorus*	Grassland	August	Subshrub	Zoochory	ND	Mid-dry	15;20;25;30;35;20/30	68.5
Asteraceae	*Moquiniastrum barrosoae*	Grassland	September	Shrub	Anemochory	ND	Dry-rainy	15;20;25;30;35;20/30	70.8
Asteraceae	*Erechtites valerianifolius*	Grassland	October	Herb	Anemochory	ND	Dry-rainy	15;20;25;30;35;20/30	93.9
Asteraceae	*Orthopappus angustifolius*	Grassland	January	Subshrub	Anemochory	ND	Mid-rainy	15;20;25;30;35;20/30	95.7
Asteraceae	*Aldama arenaria*	Grassland	February	Subshrub	Zoochory	D	Mid-rainy	15;20;25;30;35;20/30	92.0
Bignoniaceae	*Jacaranda caroba*	Grassland	November	Shrub	Anemochory	ND	Onset rainy	20;25;30	86.9
Bromeliaceae	*Ananas ananassoides*	Woodland	March	Herb	Zoochory	D	Rainy-dry	15; 20; 25; 30; 35	96.7
Bromeliaceae	*Dyckia* sp.	Grassland	January	Herb	Anemochory	ND	Mid-rainy	25;30	92.1
Calophyllaceae	*Kielmeyera coriacea*	Woodland	September	Shrub	Anemochory	ND	Dry-rainy	20; 25; 30	97.4
Cyperaceae	*Rhynchospora globosa*	Grassland	June	Herb	Autochory	D	Onset dry	20;25;30;35;20/30	84.4
Cyperaceae	*Rhynchospora rugosa*	Grassland	June	Herb	Autochory	D	Onset dry	20;25;30;35;20/30	79.8

Family	Species	Physiognomy	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)	%G
Eriocaulaceae	*Syngonanthus nitens*	Grassland	August	Herb	Anemochory	D	Mid-dry	20;25;30;20/30	4.0
Erythroxylaceae	*Erythroxylum cuneifolium*	Woodland	November	Shrub	Zoochory	ND	Onset rainy	25; 30	97.4
Fabaceae	*Anadenanthera peregrina var. falcata*	Woodland	September	Tree	Autochory	ND	Dry-rainy	15; 20; 25; 30; 35	73.3
Fabaceae	*Chamaecrista langsdorffii*	Woodland	April	Subshrub	Autochory	D	Rainy-dry	15; 20; 25; 30; 35	79.4
Fabaceae	*Dalbergia misculobium*	Woodland	August	Tree	Anemochory	ND	Mid-dry	25	100
Fabaceae	*Dimorphandra mollis*	Woodland	June	Tree	Autochory	D	Onset dry	15; 20; 25; 30; 35	67.5
Fabaceae	*Machaerium acutifolium*	Woodland	August	Tree	Anemochory	ND	Mid-dry	20; 25; 30	60.0
Fabaceae	*Mimosa sommians*	Woodland	April	Herb	Autochory	D	Rainy-dry	25	100
Fabaceae	*Plathymenia reticulata*	Woodland	August	Tree	Anemochory	D	Mid-dry	15; 20; 25; 30; 35	77.5
Fabaceae	*Stryphnodendron rotundifolium*	Woodland	August	Tree	Autochory	D	Mid-dry	15; 20; 25; 30; 35	66.7
Fabaceae	*Chamaecrista desvauxii*	Grassland	January	Subshrub	Autochory	ND	Mid-rainy	15;20;25;30;35;20/30	98.7
Fabaceae	*Crotalaria lanceolata*	Grassland	January	Subshrub	Autochory	D	Mid-rainy	15;20;25;30;35;20/30	87.9
Fabaceae	*Crotalaria incana*	Grassland	January	Subshrub	Autochory	D	Mid-rainy	15;20;25;30;35;20/30	42.2
Fabaceae	*Chamaecrista cathartica*	Grassland	January	Subshrub	Autochory	D	Mid-rainy	25	56.8
Fabaceae	*Mimosa xanthocentra*	Grassland	January	Subshrub	Autochory	D	Mid-rainy	15;20;25;30;35;20/30	74.6
Fabaceae	*Zornia latifolia*	Grassland	February	Herb	Zoochory	D	Mid-rainy	25;30;20/30	63.4
Fabaceae	*Crotalaria* sp.	Grassland	April	Subshrub	Autochory	D	Rainy-dry	25;30	19.4
Fabaceae	*Bauhinia rufa*	Grassland	June	Tree	Autochory	ND	Onset dry	15;20;25;30;35;20/30	71.6
Fabaceae	*Senna rugosa*	Grassland	June	Subshrub	Autochory	D	Onset dry	25;30;20/30	37.9
Fabaeceae	*Stylosanthes gracilis*	Grassland	March	Herb	Zoochory	D	Rainy-dry	25	14.6
Lamiaceae	*Hyptis campestris*	Grassland	June	Subshrub	Autochory	D	Onset dry	20;25;30;35;20/30	57.6
Lamiaceae	*Hyptis caespitosa*	Grassland	October	Subshrub	Autochory	ND	Dry-rainy	15;20;25;30;35;20/30	84.7
Lamiaceae	*Hyptis pulchella*	Grassland	March	Herb	Anemochory	ND	Rainy-dry	15;20;25;30;35;20/30	89.3
Lauraceae	*Ocotea pulchella*	Woodland	October	Tree	Zoochory	ND	Dry-rainy	25	80.0

Family	Species	Physiognomy	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)	%G
Loganiaceae	*Strychnos* sp.	Woodland	October	Shrub	Zoochory	D	Dry-rainy	20; 25; 30	52.6
Malpighiaceae	*Byrsonima intermedia*	Woodland	February	Shrub	Zoochory	D	Mid-rainy	25	0.0
Malvaceae	*Sida* sp.	Grassland	July	Herb	Autochory	D	Mid-dry	20;25;30;35;20/30	9.8
Malvaceae	*Byttneria sagittifolia*	Grassland	January	Subshrub	Autochory	D	Mid-rainy	25	26.5
Melastomataceae	*Leandra solenifera*	Woodland	December	Shrub	Zoochory	ND	Onset rainy	20; 25; 30	85.8
Melastomataceae	*Miconia albicans*	Woodland	December	Shrub	Zoochory	ND	Onset rainy	20; 25; 30	81.8
Melastomataceae	*Miconia fallax*	Woodland	November	Shrub	Zoochory	ND	Onset rainy	20; 25; 30	61.9
Melastomataceae	*Miconia ligustroides*	Woodland	March	Tree	Zoochory	ND	Rainy-dry	20; 25; 30	96.2
Melastomataceae	*Miconia rubiginosa*	Woodland	March	Tree	Zoochory	ND	Rainy-dry	20; 25; 30	87.2
Melastomataceae	*Tibouchina* sp.	Grassland	August	Subshrub	Anemochory	ND	Mid-dry	20;25;30;20/30	69.4
Melastomataceae	*Pleroma stenocarpum*	Grassland	August	Tree	Anemochory	ND	Mid-dry	20;25;30;20/30	68.4
Melastomataceae	*Microlicia polystemma*	Grassland	August	Subshrub	Anemochory	ND	Mid-dry	20;25;30;20/30	86.7
Melastomataceae	*Cambessedesia hilariana*	Grassland	December	Subshrub	Anemochory	ND	Onset rainy	15;20;25;30;35;20/30	84.0
Melastomataceae	*Miconia chamisois*	Grassland	September	Shrub	Zoochory	ND	Dry-rainy	20, 25, 30	82.5
Myristicaceae	*Virola sebifera*	Woodland	October	Tree	Zoochory	D	Dry-rainy	15; 20; 25; 30; 35	39.7
Myrtaceae	*Myrcia guianensis*	Woodland	November	Tree	Zoochory	ND	Onset rainy	15; 20; 25; 30; 35	91.1
Myrtaceae	*Myrcia splendens*	Woodland	January	Tree	Zoochory	ND	Mid-rainy	25	100
Myrtaceae	*Campomanesia pubecens*	Grassland	November	Shrub	Zoochory	ND	Onset rainy	15;20;25;30;35;20/30	72.8
Myrtaceae	*Eugenia pyriformis*	Grassland	November	Tree	Zoochory	ND	Onset rainy	25	100
Poaceae	*Aristida megapotamica*	Grassland	June	Herb	Autochory	D	Onset dry	20;25;30;35	65.4
Poaceae	*Gymnopogon foliosus*	Grassland	June	Herb	Anemochory	ND	Onset dry	20;25;30;35;20/30	85.3
Poaceae	*Andropogon leucostachyus*	Grassland	November	Herb	Anemochory	ND	Onset rainy	20;25;30	77.1
Poaceae	*Sporobolus aeneus*	Grassland	November	Herb	Autochory	ND	Onset rainy	15;20;25;30;35;20/30	83.3
Poaceae	*Melinis repens*	Grassland	November	Herb	Anemochory	D	Onset rainy	20;25;30;20/30	83.3
Poaceae	*Andropogon bicornis*	Grassland	February	Herb	Anemochory	ND	Mid-rainy	15;20;25;30;35;20/30	70.0

Family	Species	Physiognomy	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)	%G
Poaceae	*Digitaria insularis*	Grassland	February	Herb	Anemochory	ND	Mid-rainy	15;20;25;30;35;20/30	97.2
Poaceae	*Eustachys distichophylla*	Grassland	February	Herb	Anemochory	ND	Mid-rainy	15;20;25;30;35;20/30	97.3
Poaceae	*Loudetiopsis chrysothrix*	Grassland	March	Herb	Autochory	ND	Rainy-dry	15;20;25;30;35;20/30	87.7
Poaceae	*Tristachya leiostachya*	Grassland	March	Herb	Autochory	D	Rainy-dry	25	27.8
Poaceae	*Aristida riparia*	Grassland	April	Herb	Autochory	ND	Rainy-dry	15;20;25;30;35;20/30	82.6
Primulaceae	*Myrsine guianensis*	Woodland	November	Tree	Zoochory	D	Onset rainy	15; 20; 25; 30; 35	80.3
Rubiaceae	*Amaioua guianensis*	Woodland	June	Tree	Zoochory	ND	Onset dry	15; 20; 25; 30; 35	91.7
Rubiaceae	*Palicourea rigida*	Woodland	March	Shrub	Zoochory	D	Rainy-dry	25	0.0
Rubiaceae	*Psychotria hoffmannseggiana*	Woodland	April	Herb	Zoochory	D	Rainy-dry	15; 20; 25; 30; 35	61.8
Rubiaceae	*Coccocypselum* sp.	Woodland	April	Herb	Zoochory	D	Rainy-dry	15; 20; 25; 30; 35	34.9
Rubiaceae	*Cordiera sessilis*	Woodland	February	Tree	Zoochory	ND	Mid-rainy	15; 20; 25; 30; 35; 20/30	98.7
Siparunaceae	*Siparuna guainensis*	Woodland	February	Shrub	Zoochory	D	Mid-rainy	25	0.0
Solanaceae	*Schwenckia americana var. hirta*	Grassland	November	Herb	Anemochory	ND	Onset rainy	15;20;25;30;35;20/30	99.7
Vochysiaceae	*Qualea dichotoma*	Woodland	July	Tree	Anemochory	ND	Mid-dry	20; 25; 30	100
Vochysiaceae	*Qualea grandiflora*	Woodland	September	Tree	Anemochory	ND	Dry-rainy	15; 20; 25; 30; 35	96.0
Vochysiaceae	*Vochysia tucanorum*	Woodland	September	Tree	Anemochory	ND	Dry-rainy	20; 25; 30	90.4
Xyridaceae	*Xyris* sp1.	Grassland	June	Herb	Anemochory	ND	Onset dry	20;25;30;35;20/30	84.9
Xyridaceae	*Xyris* sp2.	Grassland	June	Herb	Anemochory	D	Onset dry	15;20;25;30;35;20/30	73.2

Herb growth form includes grass and forbs.

Table S2. Germination traits of cerrado species sampled to test seasonal synchronization and risk-reduction strategies hypothesis at Itirapina, south-eastern Brazil (ordered by family and species name) and the respective ecological and experimental information: cerrado physiognomy of seed collection, fruiting peak date (see Materials and methods section for calculations), growth form (tree, shrub, subshrub and herb), dispersal syndrome (zoochory, anemochory, autochory), dispersal season (onset rainy= November to December; Mid-rainy= January to February; rainy-dry transition= March to April; onset dry = May to June; Mid-dry = July to August; dry-rainy transition = September to October). Dormancy (ND non-dormant; D Dormant). Temperatures of the germination experiments, which were set up according to seed availability and germination percentage in optimal germination temperature (%G).

Family	Species	Physiognomy	Dispersal season	Dispersal syndrome	Dormancy	T25 (days)	T50 (days)	T75 (days)	σT	Delta-T
Araliaceae	Schefflera vinosa	Woodland	Dry-Rainy	Zoochory	D	26	32	35	0.148	4.08
Asteraceae	Chromolaena squalida	Grassland	Onset dry	Anemochory	ND	12	17,5	38	0.52	2.25
Asteraceae	Vernonanthura sp1	Grassland	Mid dry	Anemochory	D	33	117	179	0.689	7.10
Asteraceae	Elephantopus biflorus	Grassland	Mid dry	Zoochory	ND	6	6	29	0.657	7.10
Asteraceae	Moquiniastrum barrosoae	Grassland	Dry-Rainy	Anemochory	ND	18	18	39	0.368	-0.92
Asteraceae	Erechtites valerianifolius	Grassland	Dry-Rainy	Anemochory	ND	8	8	8	0	-0.92
Asteraceae	Orthopappus angustifolius	Grassland	Mid rainy	Anemochory	ND	6	6	6	0	-3.26
Asteraceae	Aldama arenaria	Grassland	Mid rainy	Zoochory	D	48	69	91	0.309	-3.26
Bignoniaceae	Jacaranda caroba	Grassland	Onset rainy	Anemochory	ND	8	8	15	0.304	-2.66
Bromeliaceae	Ananas ananassoides	Woodland	Rainy-Dry	Zoochory	D	23	23	30	0.132	7.82
Bromeliaceae	Dyckia sp1	Grassland	Mid rainy	Anemochory	ND	7	7	7	0	1.74
Calophyllaceae	Kielmeyera coriacea	Woodland	Dry-Rainy	Anemochory	ND	9	15	15	0.25	4.08
Cyperaceae	Rhynchospora globosa	Grassland	Onset dry	Autochory	D	16	26	55	0.549	12.25
Cyperaceae	Rhynchospora rugosa	Grassland	Onset dry	Autochory	D	29	54	95	0.532	12.25
Erythroxylaceae	Erythroxylum cuneifolium	Woodland	Onset rainy	Zoochory	ND	12	12	12	0	2.34

Family	Species	Physiognomy	Dispersal season	Dispersal syndrome	Dormancy	T25 (days)	T50 (days)	T75 (days)	σT	Delta-T
Fabaceae	Anadenanthera peregrina	Woodland	Dry-Rainy	Autochory	ND	4	4	22	0.692	-0.92
Fabaceae	Chamaecrista langsdorffii	Woodland	Rainy-Dry	Autochory	D	65	175	305	0.649	7.82
Fabaceae	Dalbergia miscolobium	Woodland	Mid dry	Anemochory	ND	5	7	9	0.286	7.1
Fabaceae	Dimorphandra mollis	Woodland	Onset dry	Autochory	D	53	109	187	0.558	12.25
Fabaceae	Mimosa somnians	Woodland	Rainy-Dry	Autochory	D	4	14	42	0.826	2.82
Fabaceae	Plathymenia reticulata	Woodland	Mid dry	Anemochory	D	28	77	189	0.742	7.1
Fabaceae	Stryphnodendron rotundifolium	Woodland	Mid-dry	Autochory	D	56	106	225	0.601	12.1
Fabaceae	Chamaecrista desvauxii	Grassland	Mid-rainy	Autochory	ND	10	10	24	0.412	11.74
Fabaceae	Crotalaria lanceolata	Grassland	Mid rainy	Autochory	D	47	65	147	0.516	11.74
Fabaceae	Crotalaria incana	Grassland	Mid rainy	Autochory	D	55	208	310	0.699	6.74
Fabaceae	Chamaecrista cathartica	Grassland	Mid rainy	Autochory	D	70	159	257	0.572	1.74
Fabaceae	Mimosa xanthocentra	Grassland	Mid rainy	Autochory	D	62	115	205	0.536	6.74
Fabaceae	Zornia latifolia	Grassland	Mid rainy	Zoochory	D	42	85	211	0.668	6.74
Fabaceae	Bauhinia rufa	Grassland	Onset dry	Autochory	ND	6	6	11	0.294	7.25
Fabaceae	Senna rugosa	Grassland	Onset dry	Autochory	D	11	42	63	0.703	7.25
Lamiaceae	Hyptis campestris	Grassland	Onset dry	Autochory	D	13	26	155	0.845	7.25
Lamiaceae	Hyptis caespitosa	Grassland	Dry-Rainy	Autochory	ND	4	7	11	0.467	9.08
Lamiaceae	Hyptis pulchella	Grassland	Rainy-Dry	Anemochory	ND	4	8	8	0.333	7.82
Lauraceae	Ocotea pulchella	Woodland	Dry-Rainy	Zoochory	ND	9	17	22	0.419	4.08
Loganiaceae	Strychnos sp1	Woodland	Dry-Rainy	Zoochory	D	50	95	213	0.62	4.08
Melastomataceae	Leandra solenifera	Woodland	Onset rainy	Zoochory	ND	18	18	24	0.143	-2.66
Melastomataceae	Miconia albicans	Woodland	Onset rainy	Zoochory	ND	11	17	17	0.214	-2.66
Melastomataceae	Miconia fallax	Woodland	Onset rainy	Zoochory	ND	18	18	41	0.39	-2.66

Family	Species	Physiognomy	Dispersal season	Dispersal syndrome	Dormancy	T25 (days)	T50 (days)	T75 (days)	σT	Delta-T
Melastomataceae	Miconia ligustroides	Woodland	Rainy-Dry	Zoochory	ND	19	24	26	0.156	-2.18
Melastomataceae	Miconia rubiginosa	Woodland	Rainy-Dry	Zoochory	ND	19	19	26	0.156	2.82
Melastomataceae	Miconia chamissois	Grassland	Dry-Rainy	Zoochory	ND	12	12	19	0.226	4.08
Melastomataceae	Tibouchina sp1	Grassland	Mid dry	Anemochory	ND	8	8	8	0	12.1
Melastomataceae	Pleroma stenocarpa	Grassland	Mid dry	Anemochory	ND	9	9	27	0.5	7.1
Melastomataceae	Microlicia polystemma	Grassland	Mid dry	Anemochory	ND	12	18	43	0.564	12.1
Melastomataceae	Cambessedesia hilariana	Grassland	Onset rainy	Anemochory	ND	12	15	29	0.415	7.34
Myristicaceae	Virola sebifera	Woodland	Dry-Rainy	Zoochory	D	34	168	270	0.776	9.08
Myrtaceae	Myrcia guianensis	Woodland	Onset rainy	Zoochory	ND	6	6	6	0	2.34
Myrtaceae	Myrcia splendens	Woodland	Mid rainy	Zoochory	ND	3	3	9	0.5	1.74
Myrtaceae	Campomanesia pubescens	Grassland	Onset rainy	Zoochory	ND	5	8	24	0.655	7.34
Myrtaceae	Eugenia pyriformis	Grassland	Onset rainy	Zoochory	ND	8	15	24	0.5	2.34
Poaceae	Aristida megapotamica	Grassland	Onset dry	Autochory	D	7	14	86	0.849	2.25
Poaceae	Gymnopogon foliosus	Grassland	Onset dry	Anemochory	ND	4	10	16	0.6	7.25
Poaceae	Andropogon leucostachyus	Grassland	Onset rainy	Anemochory	ND	4	8	15	0.579	-2.66
Poaceae	Sporobolus aeneus	Grassland	Onset rainy	Autochory	ND	3	7	7	0.4	7.34
Poaceae	Melinis repens	Grassland	Onset rainy	Anemochory	D	18	42	64	0.561	7.34
Poaceae	Andropogon bicornis	Grassland	Mid rainy	Anemochory	ND	21	29	87	0.611	6.74
Poaceae	Digitaria insularis	Grassland	Mid rainy	Anemochory	ND	3	3	3	0	6.74
Poaceae	Eustachys distichophylla	Grassland	Mid rainy	Anemochory	ND	3	6	6	0.333	6.74
Poaceae	Loudetiopsis chrysothrix	Grassland	Rainy-Dry	Autochory	ND	8	8	19	0.407	7.82
Poaceae	Aristida riparia	Grassland	Rainy-Dry	Autochory	ND	5	5	5	0	7.82
Primulaceae	Myrsine guianensis	Woodland	Onset rainy	Zoochory	D	116	239	363	0.516	2.34
Rubiaceae	Amaioua guianensis	Woodland	Onset dry	Zoochory	ND	28	33	41	0.188	7.25

Family	Species	Physiognomy	Dispersal season	Dispersal syndrome	Dormancy	T25 (days)	T50 (days)	T75 (days)	σT	Delta-T
Rubiaceae	Psychotria hoffmannseggiana	Woodland	Rainy-Dry	Zoochory	D	73	103	234	0.524	7.82
Rubiaceae	Coccocypselum sp1	Woodland	Rainy-Dry	Zoochory	D	148	336	462	0.515	7.82
Rubiaceae	Cordiera sessilis	Woodland	Mid rainy	Zoochory	ND	8	8	8	0	1.74
Solaceae	Schwenckia americana	Grassland	Onset rainy	Anemochory	ND	12	15	25	0.351	12.34
Vochysiaceae	Qualea dichotoma	Woodland	Mid dry	Anemochory	ND	5	7	10	0.333	7.1
Vochysiaceae	Qualea grandiflora	Woodland	Dry-Rainy	Anemochory	ND	15	15	15	0	4.08
Vochysiaceae	Vochysia tucanorum	Woodland	Dry-Rainy	Anemochory	ND	14	14	20	0.176	4.08
Xyridaceae	Xyris sp1	Grassland	Onset dry	Anemochory	ND	16	16	30	0.304	12.25
Xyridaceae	Xyris sp2	Grassland	Onset dry	Anemochory	D	18	32	90	0.667	12.2

T25= required time for germination to 25 percent of seeds; T50= required time for germination to 50 percent of seeds; T75= required time for germination to 75 percent of seeds; σT= coefficient of quartile variation of germination time. Delta-T = The difference between the temperature requirement for germination and the mean temperature during the season in which the species disperses its seeds.

Table S3. Pearson residues of Chi-squared test evaluating the relationship between dispersal season and dispersal syndrome in the cerrado species, south-eastern Brazil.

Dispersal season	Anemochory	Autochory	Zoochory
Onset rainy	0.022	**-1.530**	**1.370**
Dry-rainy	0.367	**-0.807**	0.367
Mid-dry	**2.309**	0.807	**-1.575**
Onset dry	-0.118	**1.861**	**-1.575**
Rainy-dry	**-1.869**	0.768	**1.170**
Mid-rainy	-0.413	0.459	-0.005

Chi-squared test with simulated p-value (based on 10000 replicates).
X-squared = 25.392, df = NA, p-value = 0.0042

Table S4. The logistic regression model selected according to the AIC value (Dormancy ~ Dispersal syndrome + Dispersal season).

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-3.5024	1.0547	-3.321	0.0009***
Autochory	2.4816	0.7825	3.171	0.0015**
Zoochory	2.1074	0.8044	2.620	0.0088**
Dry-rainy	0.8095	1.0730	0.754	0.4506
Mid-dry	2.5893	1.1759	2.202	0.0277*
Onset dry	2.2469	1.1278	1.992	0.0464*
Rainy-dry	2.0903	0.9852	2.122	0.0339*
Mid-rainy	1.9539	0.9870	1.980	0.0477*

Dispersal syndrome (anemochory, autochory, zoochory), dispersal seasons: Mid-rainy (January/February), Rainy-dry(March/April), Onset dry (May/June), Mid-dry (July/August), Dry-rainy (September/October), Onset rainy (November/December). Reference level= Onset rainy

Table S5. Competing phylogenetic logistic regression models tested to evaluate the relationship between dormancy and seed dispersal season, dispersal syndrome and seed mass for cerrado species, southeastern Brazil.

Modelos phyloglm	AIC	Loglik	Pen.logLik	Alpha
dormancy ~ 1	112.03	-54.02	-52.65	0.078
dormancy ~ seed mass	112.00	-53.00	-53.09	0.021
dormancy ~ phenology	111.51	-48.76	-45.11	0.023
dormancy ~ syndrome	**98.84**	-45.42	-43.11	0.06
dormancy ~ syndrome + seed mass	100.84	-45.42	-43.94	0.06
dormancy ~ syndrome x seed mass	104.47	-45.24	-48.82	0.05
dormancy ~ syndrome + phenology	102.38	-42.19	-38.42	0.051
dormancy ~ syndrome x phenology	111.72	-36.86	-47.08	0.014
dormancy ~ phenology + seed mass	112.97	-48.49	-45.61	0.022
dormancy ~ phenology x seed mass	123.44	-48.72	-58.10	0.014
dormancy ~ syndrome + phenology + seed mass	104.30	-42.15	-39.04	0.031

Phenology = Dispersal season. Syndrome = dispersal syndrome

Table S6. Comparison of the germination time among dormant species dispersing seeds during the onset of the dry season (onset-dry) with dormant species dispersing seeds in other seasons.

Hypothesis	Estimate	Est.Error	l-95%CI	u-95%CI	Evid.Ratio	Star
Onset-dry < Mid-rainy	-1.8	0.55	-Inf	-0.13	1713.3	*
Onset-dry < Rainy-dry	-0.96	0.58	-Inf	-0.02	19.9	*
Onset-dry < Mid-dry	-1.5	0.64	-Inf	-0.45	92	*
Onset-dry < Dry-rainy	-1.04	0.6	-Inf	-0.04	22.2	*
Onset-dry < Onset rainy	-1.22	0.67	-Inf	-0.13	30.1	*

Star * indicates significative difference between dispersal seasons. Reference Model: T50 ~ Dispersal season x Dormancy | Phylogeny

Ratio= Is the ratio of the posterior probability of a < b

Dispersal syndrome (anemochory, autochory, zoochory), dispersal seasons: Mid-rainy (January/February), Rainy-dry(March/April), Onset dry (May/June), Mid-dry (July/August), Dry-rainy (September/October), Onset rainy (November/December).

Table S7. The contrast between full and reduced models for germination synchrony hypothesis. Full model was: T50 ~ Dormancy x Dispersal season | Phylogeny

Model	KFOLDIC(SE)	Sigma
T50 ~ 1		0.88
T50 ~ Dormancy	**580.57 (24.24)**	**0.49**
T50 ~ Dispersal season	663.03 (26.73)	0.8
T50 ~ Dispersal season + dormancy	591.96 (24.75)	0.49
T50 ~ Dispersal season x dormancy	593.90 (27.31)	0.49
T50 ~ Dormancy - T50 ~ Dispersal season	-82.46 (12.15)	
T50 ~ Dormancy - T50 ~ Dispersal season + dormancy	-11.39 (3.96)	
T50 ~ Dormancy - T50 ~ Dispersal season x dormancy	-13.34 (8.86)	
T50 ~ Dispersal season - T50 ~ Dispersal season + dormancy	71.07 (13.54)	
T50 ~ Dispersal season - T50 ~ Dispersal season x dormancy	69.12 (14.34)	
T50 ~ Dispersal season + dormancy - T50 ~ Dispersal season x dormancy	-1.94 (7.95)	

T50= median germination time

Table S8. Comparison of Delta-T values according to dispersal season

Hypothesis	Estimate	Est.Error	95%CI	Ratio	Posterior	Star
Onset dry > Mid-rainy	3.9	1.61	(1.28, Inf)	112	0.99	*
Onset dry > Rainy-dry	2.7	1.74	(-0.18, Inf)	15.3	0.94	
Onset dry ≠ Mid-dry	-0.24	1.82	(-3.87, 3.28)	NA	NA	
Onset dry > Dry-rainy	4.78	1.71	(1.92, Inf)	475	1	*

Star * indicates significative difference between dispersal seasons (alpha=0.05). Reference Model: Delta-T ~ Dispersal season | Phylogeny

Ratio= Is the ratio of the posterior probability of a > b

Dispersal seasons: Mid-rainy (January/February), Rainy-dry (March/April), Onset dry (May/June), Mid-dry (July/August), Dry-rainy (September/October), Onset rainy (November/December).

Table S9. Bayesian phylogenetic multilevel model showing the relationship between variation of germination time and dispersal syndrome.

Group-Level: Species	Estimate	Est.Error	l-95%CI	u-95%CI	Eff.Sample	Rhat
Sd (Intercept)	0.13	0.07	0.01	0.25	302	1.01
Population-Level Effects						
Intercept	0.55	0.05	0.45	0.66	3527	1.00
Anemochory	**-0.20**	**0.07**	**-0.34**	**-0.07**	**3280**	**1.00**
Zoochory	**-0.20**	**0.07**	**-0.35**	**-0.07**	**5136**	**1.00**
Family Specific Parameters						
Sigma	0.17	0.06	0.04	0.26	210	1.01

Reference level = Autochory

Table S10. Bayesian phylogenetic multilevel model showing the relationship between variation of germination time and dispersal season.

Group-Level: Species	Estimate	Est.Error	l-95%CI	u-95%CI	Eff.Sample	Rhat
sd(Intercept)	0.15	0.08	0.01	0.26	217	1.02
Population-Level Effects						
Intercept	0.36	0.07	0.23	0.49	3310	1.00
Mid-rainy	0.01	0.09	-0.18	0.19	4054	1.00
Rainy-dry	0.01	0.1	-0.19	0.21	4387	1.00
Onset dry	**0.19**	**0.1**	**0.0**	**0.38**	**3987**	**1.00**
Mid-dry	0.12	0.11	-0.09	0.33	4004	1.00
Dry-rainy	-0.02	0.1	-0.21	0.18	3832	1.00
Family Specific Parameters						
Sigma	0.17	0.07	0.04	0.27	87	1.04

Dispersal season (Mid-rainy =January/February, Rainy-dry=March/April, Onset dry =May/June, Mid-dry =July/August, Dry-rainy =September/October, Onset rainy= November/December). Reference level= Onset of rainy season

Table S11. Bayesian phylogenetic multilevel model showing the relationship between variation of germination time and dormancy.

Group-Level: Species	Estimate	Est.Error	l-95%CI	u-95%CI	Eff.Sample	Rhat
sd(Intercept)	0.12	0.06	0.01	0.22	191	1.02
Population-Level Effects						
Intercept	0.30	0.03	0.24	0.36	3194	1.00
Dormancy	**0.28**	**0.05**	**0.18**	**0.39**	**3573**	**1.00**
Family Specific Parameters						
Sigma	0.15	0.05	0.04	0.23	134	1.03

Reference level = Non-dormant seeds

Table S12. Model comparation for risk-reduction strategies hypothesis

Model	Formula	KFOLDIC±SE	R^2±SE
1	σT~Dormancy│Phylogeny	-24.30 ± 9.38	0.64±0.24
2	σT ~Dormancy + Dispersal syndrome│Phylogeny	-24.35 ± 9.76	0.67±0.22
3	σT ~Dormancy x Dispersal syndrome│Phylogeny	-24.55 ± 8.66	0.66±0.21
1 vs 2		0.04 ± 4.43	
1 vs 3		0.25 ± 5.14	
2 vs 3		0.20 ± 3.23	

σT= variation of germination time

Table S13. Bayesian phylogenetic multilevel model showing the relationship between variation of germination time, dormancy, dispersal syndrome and interaction between dormancy and dispersal syndrome.

Group-Level: Species	Estimate	Est.Error	l-95%CI	u-95%CI	Eff.Sample	Rhat
sd(Intercept)	0.13	0.06	0.01	0.22	279	1.01
Population-Level Effects						
Intercept	0.38	0.08	0.23	0.54	2166	1.00
Anemochory	-0.08	0.09	-0.25	0.09	2510	1.00
Zoochory	-0.10	0.09	-0.29	0.08	2196	1.00
Dormancy	**0.27**	**0.10**	**0.08**	**0.46**	**2500**	**1.00**
Anemochory:Dormancy	0.01	0.15	-0.19	0.39	3927	1.00
Zoochory: Dormancy	-0.08	0.13	-0.34	0.17	2974	1.00
Family Specific Parameters						
Sigma	0.13	0.06	0.02	0.22	178	1.02

Reference levels = Non dormant seeds and autochory

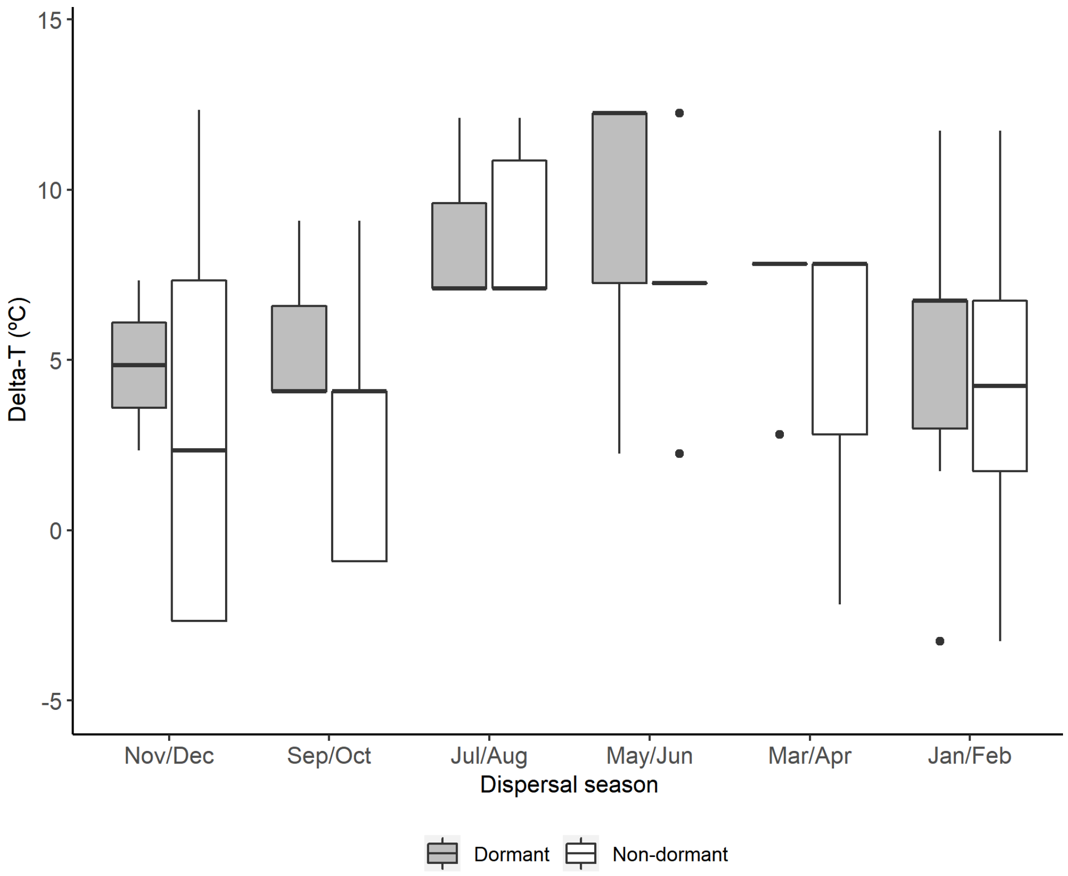

Fig S1. Relationships between Delta-T, dormancy and dispersal season. Delta-T is the difference between minimal optimal germination temperature and local temperature. Lows values of Delta-T indicates that weather does not constraint the germination, while under high values of Delta-T the germination does not occur. Germination period is the onset of rainy season or Onset rainy (November/December). Dispersal seasons: Mid-rainy (January/February), Rainy-dry (March/April), Onset dry (May/June), Mid-dry (July/August), Dry-rainy (September/October), Onset rainy (November/December).

CAPÍTULO 3

How do regenerative traits vary among Cerrado habitats?

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How do regenerative traits vary among Cerrado habitats?

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Abstract

Regenerative traits are crucial to understand patterns and processes in plant communities. However, regenerative traits are underrepresented in community ecology preventing a better assessment of trait-based community assembly. The Brazilian savannas (Cerrado) are composed by a mosaic of physiognomies, from open to closed savannas, that show a great variation in regenerative traits. Here we assessed habitat-related regenerative traits by comparing species from open and closed savannas. We classified 82 species according to dormancy (non-dormant, PD, PY, PDPY, MD, MPD), dispersal syndrome (autochory, anemochory, exozoochory, endozoochory), and dispersal season (rainy, dry, rainy-to-dry and dry-to-rainy transitions). We determined germination percentage, mean germination time and variation of germination time in conditions of optimal temperatures, and seed mass. Principal coordinates analysis (PCoA) with Gower's distance were used to explore the relationships between regenerative traits and habitat. The two main axes of the PCoA explained 38% of the total variance. The first axis was related to germination traits (germination percentage, mean gemination time, and variation of gemination time) and separated dormant from non-dormant species, whereas the second axis was related to seed mass, growth form, and dispersal syndromes which sharply separated open and closed savanna species. Unexpectedly, seed germination and dormancy traits did not differ among open and closed savanna species. Thus, in the Cerrado, seasonality is a strong filter for both germination and seedling establishment with species shaping germination strategies regardless of habitat. The most common strategy was dispersing non-dormant seeds in the rainy season, while the least common strategy was dispersing seeds during the rainy-to-dry season transition but remaining dormant until the beginning of the next rainy season. We suggest that germination and seasonality should be taken into account for any restoration or conservation plans in seasonal savannas.

Keywords: Regeneration traits, Neotropical savanna, seed dormancy, environmental heterogeneity, trait-based community assembly.

Introduction

Regeneration traits can be defined as traits that affect the outcome of plant regeneration processes, such as seed dispersal capacity, persistence, germination, and seedling establishment (Larson & Funk 2016, Saatkamp et al. 2019). Regeneration traits determine not only seedling survival and plant distribution patterns, but also the environmental conditions faced by plants after establishment (Donohue et al. 2010, Saatkamp et al. 2014, Tamme et al. 2014, Rosbakh & Poschlod, 2015). Even though regeneration traits are key to understand plant community dynamics, including species coexistence and how environmental filters act on regional species pool in assembling communities, they are historically underrepresented in community assembly studies (Keddy et al. 1992, Jiménez-Alfaro et al. 2016, Larson & Funk 2016, Tudela-Isanta et al. 2018). However, understanding the processes involved in community assembly, as well as what drives community composition and species distribution, would be significantly improved if regeneration traits were included in such studies (Lavorel & Garnier 2002, Larson & Funk 2016).

Except for seed mass, the variation of regenerative traits between and within communities remains unclear (Larson & Funk 2016, Moles 2018, Saatkamp et al. 2019). However, seed germination timing, dormancy, seed dispersal and dispersal phenology are relevant to understanding plant recruitment and species coexistence (Grubb 1977, Keddy 1992, Ramos et al. 2017, Escobar et al. 2018), and how these traits vary with the environment may reflect their adaptative value (Finch-Savage & Leubner-Metzger 2006, Willis et al. 2014, Liu et al. 2017). At the global scale, seed mass decreases and dormancy increases with increasing seasonality (Moles & Westoby 2004, Rubio de Casas et al. 2017). Moreover, in seasonal environments, seed release and germination peaks are synchronized with the onset of the favorable season for seedling establishment (Garwood 1983, Bhat & Murali 2001, Escobar et al. 2018). At the local scale, regenerative traits shift with environmental heterogeneity, thus in environments with high spatial heterogeneity, seed dispersal is selected against dormancy or large seeds, while in environments with high temporal heterogeneity or with high competition, dormancy and large seeds are selected against seed dispersal (Venable & Brown 1988, Rees 1996, Buoro & Carlson 2014).

The Brazilian savannas (Cerrado) are a biodiversity hotspot (Myers 2000) composed of a dynamic mixture of woody (trees and shrubs) and ground layers (subshrubs, forbs and grasses) that result in a mosaic of different physiognomies ranging from open to closed savannas (Oliveira-Filho & Ratter 2002). This spatial heterogeneity creates suitable conditions to test the role of different selective pressures on the evolution of seed traits. Open savannas are characterized by a continuous herbaceous layer with scattered shrubs and subshrubs and, at the opposite extreme of this *continuum*, closed savannas are dominated by trees and shrubs with a discontinuous herbaceous layer. Thus, the Cerrado vegetation shows a huge variation in environmental conditions, where habitats differ in light and nutrient availability, disturbance frequencies, groundwater depth, soil water deficits in upper soil layers, amount of leaf litter (Oliveira-Filho & Ratter 2002, Rossatto et al. 2012, Salazar et al. 2012), growth forms, and regeneration traits (Oliveira-Filho & Ratter 2002, Batalha & Martins 2002, Gottsberger & Silberbauer-Gottsberger 2006, Oliveira 2008, Simon et al. 2009, Kuhlmann & Ribeiro 2016, Escobar et al. 2018). Such variation in environmental conditions provide an ideal context to assess habitat-related regeneration traits.

Regeneration traits related to seed production and dispersal (i.e., seed mass, dispersal phenology, and dispersal syndrome) differ with plant growth forms (Ramirez 2002, Moles et al. 2005, Gottsberger & Silberbauer-Gottsberger 2006, Kuhlmann & Ribeiro 2016) and the proportion of growth forms varies among Cerrado physiognomies (Batalha & Martins 2002, Oliveira-Filho & Ratter 2002). Thus, in closed savannas, seed dispersal occurs mainly at the end of the dry season and at the beginning of the rainy season and occurs predominantly by animals (>60% of species; Gottsberger & Silberbauer-Gottsberger 2006, Pirani et al. 2009, Kuhlmann & Ribeiro 2016). Autochory and anemochory are the predominant dispersal syndrome in open savannas and seeds are dispersed mostly at the end of the rainy season and beginning of the dry season (Batalha & Mantovani 2000, Ramirez 2002, Batalha & Martins 2004, Gottsberger & Silberbauer-Gottsberger 2006, Tannus et al. 2006, Munhoz & Felfili 2007, Oliveira 2008, Pirani et al. 2009, Kuhlmann & Ribeiro 2016).

In Neotropical savannas, many studies have found that regeneration traits, such as dispersal phenology and dispersal syndromes, vary with habitat type (open and closed savannas) and growth forms (Batalha & Mantovani 2000, Ramirez 2002, Batalha & Martins 2004, Gottsberger & Silberbauer-Gottsberger 2006, Kuhlmann & Ribeiro 2016). However, studies that address other regeneration traits (such as seed germination, seed dormancy, and seed mass) are scarce, especially at the community level where studies are mostly restricted to certain families and growth forms (Salazar et al. 2011, Ramos et al. 2017) or involve only one habitat type (Escobar et al. 2018). This prevents a more complete understanding of how these traits vary throughout broad ecological gradients in Neotropical savannas. Here, we aimed to evaluate the relationship between seed-based regeneration traits, habitat type, and growth forms in contrasting savanna environments of the Cerrado. Specifically, we determined dispersal phenology, dispersal syndrome, seed mass, percentage of germination, germination time, variation of germination time, seed dormancy, and dormancy class for 82 Cerrado species (48 species from open savannas and 34 species from closed savannas) that occur in the same macro-climatic region.

We expect that each habitat type shows a unique set of regeneration traits that will be related to differences in micro-climate, soil types, and/or disturbance regime. Thus, we expect a larger proportion of dormant species in open savannas because of the higher unpredictability and drought severity (Salazar et al. 2012, Daibes et al. 2019). Moreover, during the rainy season, variation in water availability on upper soil layers is greater in open savannas (Kanegae et al. 2000), favoring an increase in the variation of germination time (Veenendal et al. 1996). We also expect a greater delay in germination (increase of germination time) in seeds from open savannas species, given that these species tend to fruit during periods favorable for germination but not for seedling establishment (Munhoz & Felfili 2007, Oliveira 2008, Tannus et al. 2006). In contrast, lower environmental unpredictability in closed savannas should select non-dormant species because of the costs associated with the evolution of dormancy (Dayrell et al. 2017). Finally, we expect that seed dormancy and dormancy class will vary with growth forms, with trees having a smaller proportion of dormant species in relation to forbs and grasses, and with physiological dormancy being more common among forbs and grasses and physical dormancy among woody species (Baskin & Baskin 2014).

Material and Methods

Study Area

The study was conducted in two areas (*Fazenda Botelho* and *Estação Ecológica de Itirapina*) of Cerrado (Oliveira-Filho & Ratter 2002), located at Itirapina, São Paulo State, Southeastern Brazil (22° 13’ a 22° 10’S; 47° 55’ a 47° 51’W), about 3 km apart from each other. The vegetation of *Fazenda Botelho* is a closed savanna (locally known as *cerrado stricto sensu*), characterized by a dominant woody layer with a tree height ranging between 3 and 12 m, a discontinuous canopy cover of 30 to 90% and a scattered herbaceous layer (Reys et al. 2013, Camargo et al. 2013). The *Estação Ecológica de Itirapina* comprises different open savanna physiognomies (locally known as *campo limpo* and *campo sujo*), characterized by a dominant herbaceous layer (mainly grasses and forbs) and scattered shrubs and subshrubs (Tannus et al. 2006). The climate at both sites, hereafter referred as closed savanna and open savanna, is seasonal and the year can be divided into four seasons: a hot and rainy season (November to March), a rainy-to-dry transition (April), a cold and dry season (from May to August), and a dry-to-rainy transition (September to October; Escobar et al. 2018). Mean annual precipitation is 1513 mm and mean annual temperature is 20.8°C, with an average minimum temperature of 9°C in July and an average maximum temperature of 30°C in February (Escobar et al. 2018).

Fruit and seed collection

In the closed savanna, mature fruits from 34 species were collected every 15 days from March 2015 to March 2016. In the open savanna areas, mature fruits from 48 species were collected every month between June 2016 and June 2017 (Supplementary Table S1). Here we examined seeds from 82 species and 26 families, including major lineages of angiosperm (Magnoliids, Monocots, and Eudicots) and a broad spectrum of growth forms: forbs and grasses, subshrubs, shrubs, and trees (Supplementary Table S1). We randomly followed trails inside both areas, collecting all fruiting species available. Fruits of at least 10 individuals of a given species were collected, placed into paper bags and taken to the laboratory where seeds were removed up to 48 hours after harvesting. Seeds were then dried for 48 hours at 25°C and 40% relative humidity. Seeds were stored in such conditions for less than three weeks prior to the germination experiments (see Escobar et al. 2018).

Species functional traits

Plant regenerative traits used in our analyses are described below and have followed the classification proposed by Pérez-Harguindeguy et al. (2013). We classified the species based on field observations, results from experiments, and the literature.

Growth forms

Based on field observations, species were classified in four growth forms: herbaceous (grasses and forbs), subshrubs (plants with long-lived woody roots growing belowground or with multiple, ascending woody stems that are less than 1m tall), shrubs (woody plants between 1 and 3m tall with canopies typically carried by several trunks), and trees (woody plants usually >5m tall with the main canopy elevated on a long-lived, substantial, usually single trunk; adapted from Pérez-Harguindeguy et al. 2013).

Dispersal syndrome

Species' dispersal syndromes were classified as endozoochory (zoochory as in Escobar et al. 2018), exozoochory (unintentional seed dispersal by animals), anemochory (wind dispersal), and autochory (combining unassisted dispersal and ballistichory) based on morphological characteristics of the diaspores, field observations, and information extracted from the literature (Morellato & Leitão-Filho 1992, Oliveira & Moreira 1992, Batalha & Mantovani 2000, Weiser & Godoy 2001, Tannus et al. 2006; Camargo et al. 2013, Escobar et al. 2018), following the system proposed by Pérez-Harguindeguy et al. (2013). Species with minute dust-like seeds with a fresh mass of <0.1 mg (Oliveira & Garcia 2011, Dugarte et al. 2015, Giorni et al. 2018), were considered as anemochorous; species lacking structures known to facilitate wind or animal dispersal and with seed mass ≥ 0.1 mg were classified as autochorous (Pérez-Harguindeguy et al. 2013).

Seed mass

To determine species fresh seed mass, 100 recently harvested seeds were weighed individually (for seeds weighing >0.001 g) or in eight groups of 100 seeds each (for seeds weighing <0.001 g) with an analytical scale (Ohaus, Pioneer PA214; Ohaus, New Jersey, USA).

Dispersal phenology

For 24 out of the 34 species collected in the closed savanna, the fruiting peak was determined based on the 11-year database (2005–15) of the Phenology Laboratory at the University of São Paulo (UNESP; Escobar et al. 2018). For the remaining species, the fruiting peak was determined based on the seed collection dates, which were carried out throughout 2015, 2016, and 2017. Fruiting peak dates were used to determine seed dispersal season of species, according to Escobar et al. (2018): dry season (May to August), rainy season (November to March), dry-to rainy transition (September to October) or rainy-to-dry transition (April).

Seed germination experiments

For the germination experiments, seeds were placed in Petri dishes with two layers of filter paper saturated with distilled water under 24-h white light (≈32 µmol m−2 s−1), and up to five constant temperatures (Supplementary Table S1). For each species, we used six replicates containing 20–25 seeds at each temperature according to seed availability. Germination was determined by radicle curvature or protrusion of aerial structures (Northam & Callihan 1994), except for dust-like seeds, in which germination occurred through the protrusion axis of the embryo (Dugarte et al. 2015). The experiments were monitored three times a week for one month, after which germination was monitored weekly for a maximum of 12 months or until the germination curve was stabilized (at least 4 weeks without germination; Sautu et al. 2006). At the end of the experiment, viability of non-germinated seeds was analyzed by means of the tetrazolium test, using 1 % solution at 30 °C for 48–72 h (ISTA 2007).

Based on the germination experiments we determined the percentage of germination, mean germination time, and standard deviation of germination time at optimal temperature conditions according to Ranal & Santana (2006). We used the coefficient of variation of germination time as a measure of variation of germination time which was calculated by dividing the standard variation of germination time over the mean germination time. Optimal temperature for germination for each species was defined as the temperature or array of temperatures with the highest germination percentage and germination rate.

Seed dormancy

Species were classified as non-dormant (ND) or into five dormancy classes according to Baskin & Baskin (2014): physical dormancy (PY), species with impermeable seed coats, well-developed and non-dormant embryos (germination occurs within 30 d after physical scarification); morphological dormancy (MD), species with seeds containing undeveloped embryos and a mean germination time of less than 30 days; morphophysiological dormancy (MPD), seeds with undeveloped embryos and a mean germination time of over 30 days; physiological dormancy (PD), seeds that are permeable to water, with well-developed embryos and a mean germination time >30 d; and physiophysical dormancy (PYPD), seeds that are impermeable to water and have physiological dormancy. Seed permeability and embryo growth were determined before germination according to Escobar et al. (2018).

Statistical analyses

To explore the relationships between the regenerative traits (i.e. dispersal phenology, dispersal syndrome, seed mass, percentage of germination, germination time, variation in germination time, dormancy, and dormancy classes), growth forms, and habitat, we calculated the global distance matrix (Pavoine et al. 2009) based on the variables mentioned above and then applied a Principal Coordinates Analysis (PCoA) using Lingoes transformation (Lingoes 1971). We used the first two main axes of variation given that the eigenvalues decreased sharply from the third axes. To visualize the groups based on the categorical variables, we plotted a factorial map according to Pavoine et al. (2009). These analyses were performed with the package *ade4* (Dray & Dufour 2007) in R software (R Development Core Team, 2016). Correlations between traits in terms of (squared) distances between species and contributions of traits to the global distance were estimated with the function *kdist.cor* of the package *ade4* in R (Dray & Dufour 2007). Magnitude and significance of correlations between traits and PCoA axis 1 and 2 were tested with Spearman's correlation coefficient for continuous variables and with a linear model for discrete variables.

Since the PCoA suggested a weak relationship between dispersal phenology, variation of germination time and dormancy classes with habitat types (closed and open); and between seed mass, phenology, and dispersal syndrome with dormancy status (presence/absence), we explored these relationships with two logistic regressions: 1) habitat ~ dispersal season + dormancy classes + variation of germination time; and 2) dormancy ~dispersal season + dispersal syndrome + seed mass. We then selected the models with the lower Akaike information criterion (AIC) using the function *step* (Venables & Ripley 2002) and tested the significance with a chi-square test in R software (R Core Development Team 2016). We also tested the relationship between dormancy status and growth forms by a logistic regression (Dormancy ~ growth form); and between growth form and dormancy class by a chi-square test in R software (R Core Development Team 2016).

Results

Regeneration traits across savannas

Seed mass ranged between 0.00001 and 0.64g, with most of open savanna seeds weighing between 0.0001 and 0.01g and most closed savanna seeds weighing between 0.01 and 0.1g (Fig. 1A). Most species (>66%) showed high germination percentage (>70%) in both habitats (71.4 ± 31.5 and 71.2 ± 25.3 average germination ± standard deviation in closed and open savannas, respectively), and just four species did not germinate. Mean germination time ranged from 3.7 and 191.3 days, but most species (>60%) germinated in less than 30 days in both habitats (Fig 1B); average germination time was similar in closed and open savannas (41.1 ± 46.5 and 28.8 ± 29.3, respectively). The coefficient of variation in germination time ranged from 0 to 66.6%, and open savanna species tended to show higher values (19.4±15%, mean ± standard deviation) than closed savanna species (15±10.5%). In both habitat types, more than half of species were non-dormant (53 and 57% in closed and open savannas, respectively), followed by physiological and physical dormancy (Fig. 1C). Morphological and morphophysiological dormancy were registered in four closed savanna species, while physiophysical dormancy was represented by one open savanna species (Fig. 1C).

We also found interspecific variation in dispersal phenology. Seed dispersal occurred throughout the year and showed similar patterns in both habitats: most species dispersed seeds at the onset of the rainy season, while few species were dispersing seeds during the rainy-to-dry season transition (Fig. 2). However, the open savanna showed a greater proportion of species dispersing seeds during the dry season than the closed savanna (Fig. 2). The proportion of dispersal syndromes differed with habitat types (Fig. 2): endozoochory was the main syndrome (>65% species) in closed savannas followed by anemochory and autochory (20% and 15%, respectively). In the open savanna, anemochory and autochory (46 and 40% species, respectively) were the dominant dispersal syndrome, and zoochory was poorly represented (6% endozoochory and 8% exozoochory; Fig. 2B). Additionally, exozoochory occurred just in 5% of species in the open savanna (Fig. 2D).

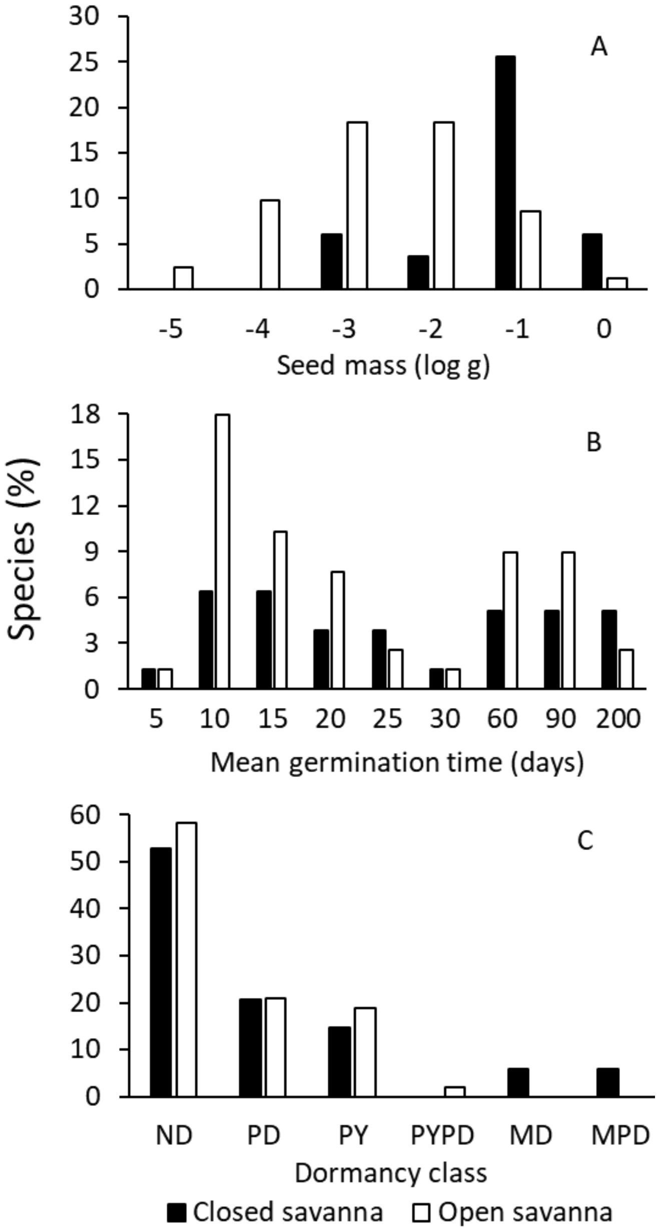

Figure 1. Relationships between habitat type (open and closed) and seed mass (A), mean germination time (B), and dormancy classes for 82 savanna species from southeastern Brazil.

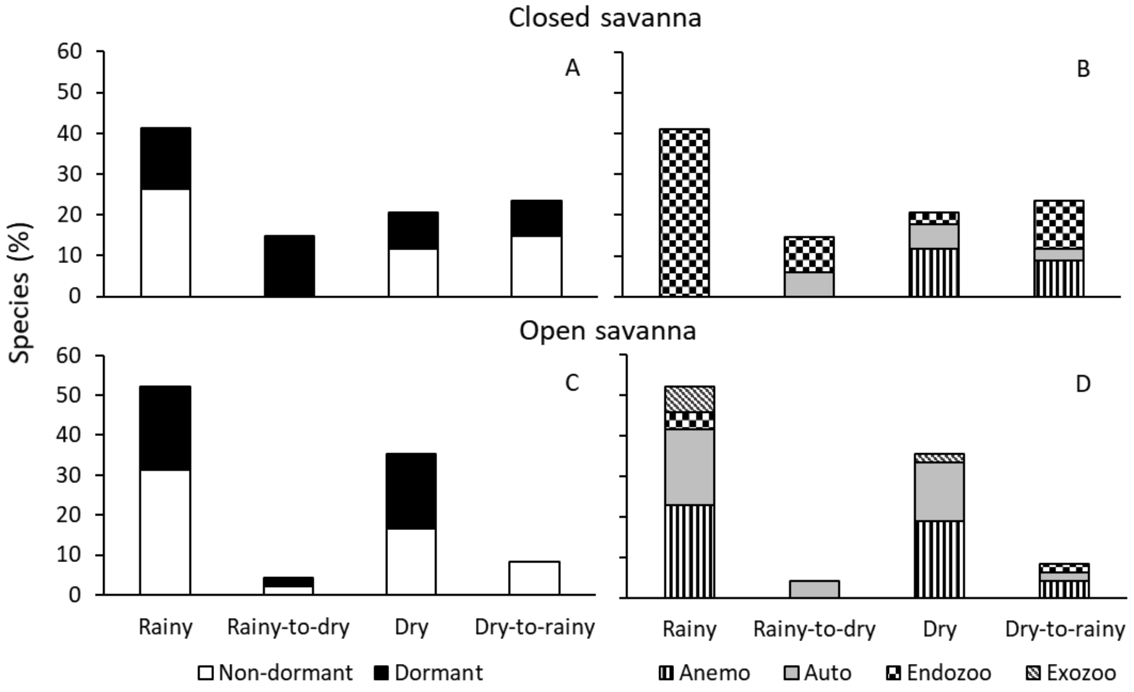

Figure 2. Relationship between dispersal season (B, D) and dormancy (A, C) for closed (upper) and open (lower) savannas from southeastern Brazil.

Habitat-related regeneration traits

Correlation between the squared distances of savanna species obtained for pairwise variables showed that habitat type correlate more strongly with dispersal syndrome, seed mass, and growth form than other variables, while seed dormancy correlate more strongly with all germination traits (percentage of germination, germination time, and coefficient of variation of germination time) and dispersal syndrome in comparison to other variables (Fig. 3). Additionally, dispersal season did not show strong correlations with any of the variables. The main variables contributing to explain the differences among savanna species were dormancy, dormancy classes, habitat, dispersal syndrome, and percentage of germination. Growth form and coefficient of variation of germination time showed an intermediate importance, while germination time, dispersal season, and seed mass showed a weak correlation with the global distance between species (Table 1).

Table 1. Relative contribution of each variable to the global distance between savanna species. The contribution of each variable in explaining the differences between species increases as its correlation with the global distance increases.

Variable	Correlation with global distance
Dormancy class	0.66
Dormancy	0.62
Habitat	0.47
Dispersal syndrome	0.46
Germination (%)	0.45
Growth form	0.4
Variation of GT	0.4
Germination time	0.37
Dispersal season	0.31
Seed mass	0.24

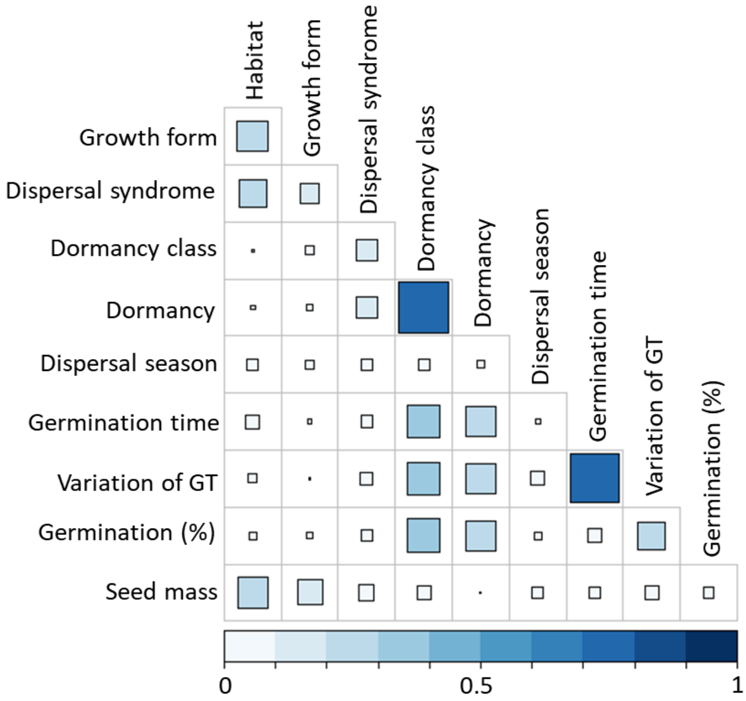

Figure 3. Correlation matrix between the squared distances of savanna species obtained for pairwise variables. We used absolute values because negative or positive correlations between categorical variables are not ecologically meaningful. Germination time = Mean germination time; Variation of GT = variation coefficient of germination time. Magnitude of the correlations are represented by the intensity of the colors and the size of the squares.

Contrary to our expectations, seed dormancy, mean germination time, and the variation of germination time were not correlated to habitat (Figs. 1B, C, Fig. 3, Table 5). The first PCoA axis mainly separated dormant and non-dormant species, while the second axis mainly separated open savanna species from closed savanna species (Fig. 4, Table 2), and these two axes together explained 38% of the global distance between species (Fig. 4). The percentage of germination, the mean germination time, and the variation of germination time were strongly correlated to the first PCoA axis (Table 2), indicating that dormant species show the lowest germination percentage, with slower germination times, and a more variable germination than non-dormant species. Seed mass, dispersal syndrome, and dispersal season also correlated with the first axis. Although such correlation was weak (Table 2), it suggests that the probability of having dormant seeds was higher in species dispersing during the rainy-to-dry transition and that seeds from anemochorous species are lighter and less likely to be dormant in comparison to species with other dispersal syndromes (Table 2, Fig. 4).

The AIC stepwise model selection indicated that seed dormancy varied with dispersal syndrome. However, seed dormancy also varied significantly with dispersal season, but not with seed mass (Table 3). Thus, the likelihood of having dormant seeds was lowest in species dispersed during the dry-to-rainy transition, while the chances of having dormant seeds in species dispersing during the dry season was similar to that of species dispersing in any other season (Table 4, Fig. 4). Moreover, in anemochorous species, the likelihood of seeds being dormant was lower than in species showing other dispersal syndromes (Fig. 4). The variation in seed mass observed throughout the first PCoA axis was related to dispersal syndrome and not to dormancy (Fig. 3).

On the other hand, growth form, seed mass, and dispersal syndrome were strongly associated to the second PCoA axis. Thus, in closed savannas, endozoochorous shrub and tree species with heavier seeds dominate, while in open savannas, anemochorous and autochorous subshrub and herbaceous species dominate (Table 2, Fig. 4). Variation in germination time, dormancy class, and dispersal season were also correlated with the second axis (Table 2). Although the correlation was weak, it suggests that variation in germination time, seed dispersal during the dry season, and physical dormancy was higher in open than closed savanna species (Fig. 2, Table 2). According to the stepwise model selection, habitat types differed regarding to dispersal season but not dormancy class nor variation of germination time (Table 5). Thus, the proportion of open savanna species dispersing seeds during the dry season was greater than during the dry-to-rainy transition, while such proportion was similar among closed savanna species (Table 6, Fig. 4). The correlation between the variation in germination time and dormancy class with the second

PCoA axis seems to be more related to dispersal syndrome or season that with habitat type (Fig. 1 and 3).

Table 2. Correlation coefficients between regeneration and vegetative traits of 82 savanna species and PCoA axis 1 and 2. Significant correlations are given in bold. Correlations were tested with Spearman's correlation coefficient for continuous variables and with linear models for discrete variables. Germination time= Mean germination time; Variation of GT= coefficient variation of germination time.

Variables	PCoA axis 1 Correlation (p-values)	PCoA axis 2 Correlation (p-values)
Seed mass	-0.44 (<**0.001**)	-0.58 (<**0.001)**
Germination time	-0.69 **(<0.001**)	0.16 (0.15)
Variation of GT	-0.75 (<**0.001**)	0.3 (**0.008**)
Germination	0.63 (<**0.001**)	-0.2 (0.07)
Habitat	0.02 (0.093)	0.82 (<**0.001**)
Growth-form	0.024 (0.587)	0.73 (<**0.001**)
Dispersal syndrome	0.31 (<**0.001**)	0.63 (<**0.001**)
Dispersal season	0.1 (**0.012**)	0.12 (**0.005**)
Dormancy	0.93 (<**0.001**)	0.01 (0.16)
Dormancy class	0.93 (<**0.001**)	0.1 (**0.021**)

Table 3. Competing logistic regression models evaluated the relationship between dormancy and dispersal season, dispersal syndrome, and seed mass for different savanna types from southeastern Brazil. The chosen model is given in bold. According to lowest AIC criteria the best model was dormancy ~ dispersal syndrome, however we choose the model dormancy ~ dispersal syndrome + dispersal season because dormancy differs significantly (p<0.005) from both variables and the AIC value is similar in both models.

Model	Deviance	AIC	P
Dormancy~ dispersal season + dispersal syndrome + seed mass	88.64	104.6	0.962
Dormancy~ dispersal season + dispersal syndrome	**88.64**	**102.6**	**0.001**
Dormancy~ dispersal season	104.48	112.5	0.046
Dormancy~ dispersal syndrome	94.43	102.4	<0.001
Dormancy~ seed mass	112.45	116.4	0.93
Dormancy~ 1	112.45	114.4	

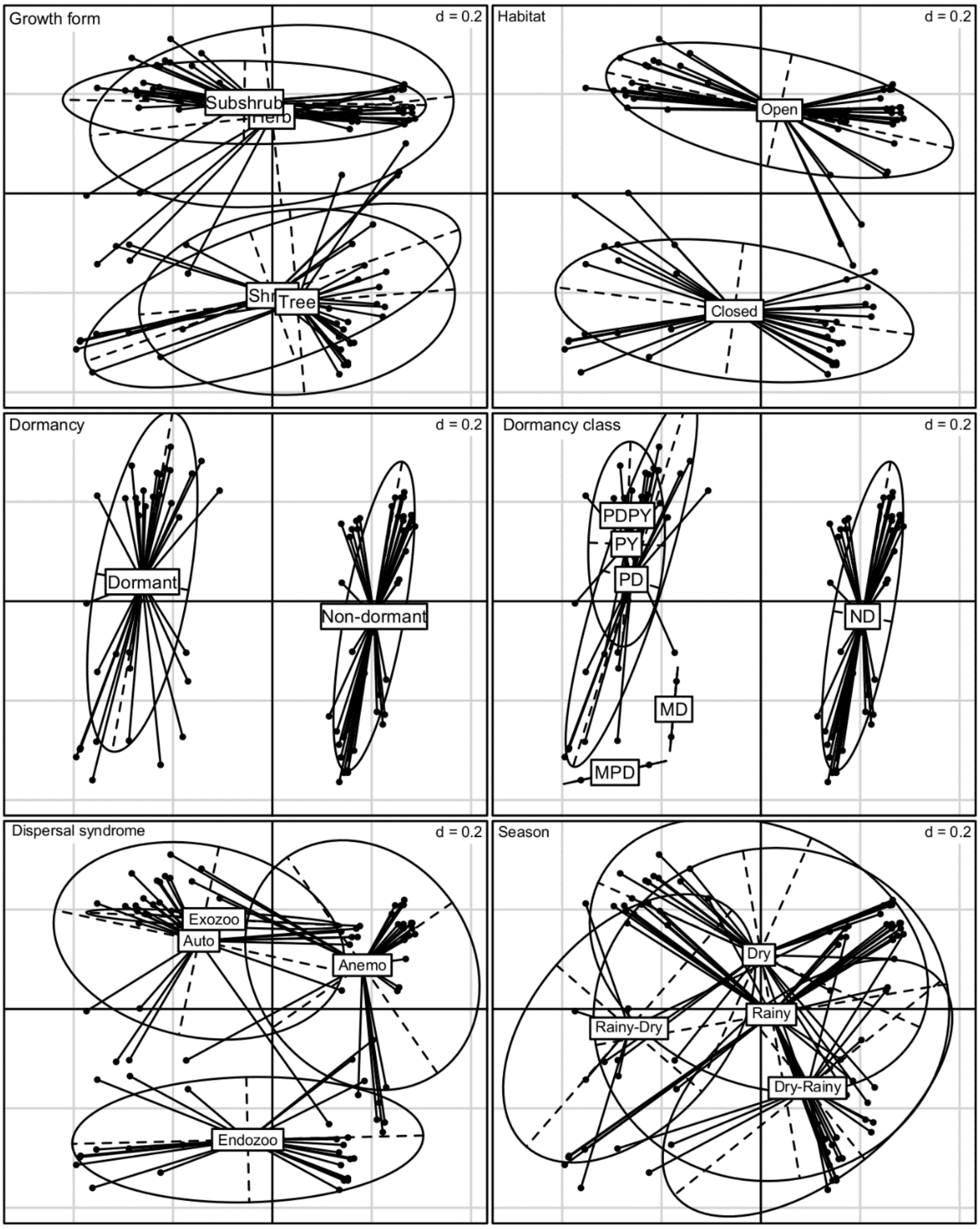

Figure 4. Principal coordinates analysis (PCoA) applied to the global distance metric using growth form, habitat type, and regenerative traits for 82 species from a closed and open savanna. Each panel shows a factorial plot representing the levels of each categorical variable at the centroid of species assigned to each level. Axis 1 explains 20.7 % of the variation and axis 2 explains 17.3%. Vertical and horizontal grid lines are separated by 0.2 units (d) at each axis.

Table 4. Results of the logistic regression used to test if seed dormancy depends on dispersal season and dispersal syndrome in savanna species from southeastern Brazil. Model: Dormancy ~ dispersal season + dispersal syndrome. Reference level: Rainy-to-dry season transition and anemochory.

Coefficients	Estimate	Std. error	Z value	P value
Intercept	0.2374	1.2797	0.186	0.853
Dry	1.792	1.155	1.552	0.121
Dry-to-rainy	2.890	1.269	2.277	**0.023**
Rainy	2.262	1.129	2.003	**0.045**
Autochory	-2.4066	0.7207	-3.339	**<0.001**
Exozoochory	-2.9574	1.3212	-2.238	**0.025**
Endozoochory	-1.6451	0.7659	-2.148	**0.032**

Significant differences are given in bold.

Table 5 Competing logistic regression models evaluating the relationship among habitat types, seed dispersal season, and dormancy class for savanna species from southeastern Brazil. The chosen model (lowest AIC values) is given in bold.

Model	Deviance	AIC	P value
Habitat~dispersal season + dormancy class + variation of germination time	84.674	104.7	0.37
Habitat~dispersal season + variation of germination time	90.053	100	0.08
Habitat~dispersal season	**91.415**	**99.4**	**0.052**
Habitat~ variation of germination time	96.684	100.7	0.22
Habitat~ dormancy class	92.9	103.2.	0.13
Habitat~ 1	98.163	100.2	

Table 6. Results of logistic regression comparing open and closed savannas in relation to dispersal season (model: habitat~ dispersal season).

Coefficients	Estimate	Std. error	Z value	P value
Intercept	-0.8873	0.4491	-1.976	0.048
Dry-to-rainy	**1.5805**	**0.7594**	**2.081**	**0.037**
Rainy	0.3075	0.5596	0.550	0.583
Rainy-to-dry	1.8036	0.9496	1.899	0.058

Reference level: dry season. Significant differences are given in bold.

Dormancy and growth-form

The proportion of dormant species was not significantly related to growth forms (Fig. 3 and 4), which was confirmed by a logistic regression (Table 7). On the other hand, dormancy class was associated with growth forms (X^2, p=0.021), such that herbaceous species and physiological dormancy, subshrubs and physical dormancy, trees and non-dormancy were more associated to each other than expected by chance. Shrubs and physical dormancy and trees and physiological dormancy species were less associated than expected by chance (Table 8, Fig. 5). Additionally, morphophysiological dormancy was only observed in trees, physiophysical dormancy was only observed in subshrubs, and morphological dormancy was only observed in herbaceous and shrub species. Species with physiophysical (one species), morphophysiological (two species), and morphological (two species) dormancy were excluded from the test due to their low occurrence. Morphophysiological dormancy was only observed in trees, physiophysical dormancy in subshrubs, and morphological dormancy in herbaceous and shrub species.

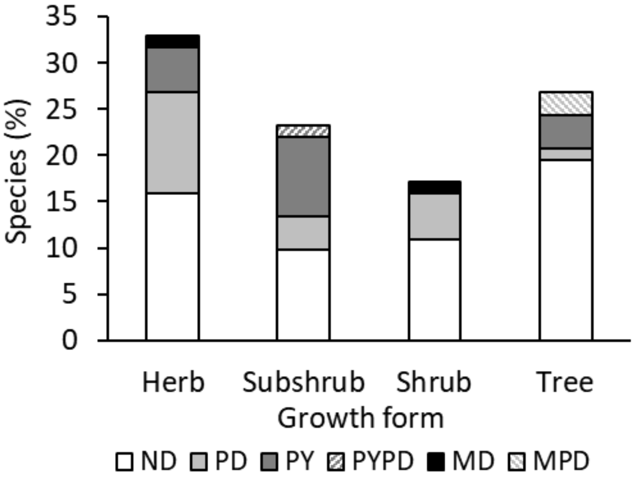

Figure 5. Relationship between dormancy class and growth forms. ND = non-dormant, PD = physiological dormancy, PY = physical dormancy, PYPD = physiophysical dormancy, MD= morphological dormancy, MPD = morphophysiological dormancy.

Table 7. Results of the logistic regression comparing dormancy in relation to growth forms for 82 savanna species from southeastern Brazil. Reference level: tree

Coefficients	Estimate	Std. error	Z value	P value
Intercept	0.9808	0.4787	2.049	0.04
Herbaceus	-1.0549	0.6144	-1.717	0.086
Shrub	-0.3930	0.7350	-0.535	0.593
Subshrub	-1.2993	0.6671	-1.948	0.051

Table 8. Pearson residuals of the chi-square (X^2) test between growth forms and dormancy class for 82 savanna species from southeastern Brazil.

Growth form	Non-dormant	Physiological dormant	Physical dormant
Tree	1.172	-1.625	-0.334
Shrub	0.443	0.667	-1.537
Subshrub	-0.84	-0.489	2.06
Herbaceus	-0.643	1.361	-0.334

Discussion

One of the main hypotheses related to the evolution of dormancy states that dormancy is selected where seasonality and environmental uncertainty are high (Baskin & Baskin 2014). Thus, we expect a greater proportion of dormant species in open savanna areas, where fire frequency and probability of droughts are greater. However, our results showed that dormancy, germination percentage, mean germination time, and variation of germination time did not differ between open and closed savannas, indicating that climatic seasonality is a strong filter for germination and establishment in savanna plant communities and that species show similar germination strategies regardless of habitat. On the other hand, seed mass and the proportion of growth forms and dispersal syndromes did differ between habitats, suggesting that such traits are related to differences in local microclimate, soil or disturbance frequency. Finally, we did not find a significant relationship between dormancy and growth forms. Nonetheless, the proportion of dormant species tended to be smaller among tree and shrubs (27 and 36%, respectively) in relation to subshrubs and herbaceous species (58 and 52%, respectively). Additionally, physiological dormancy was more commonly found among herbaceous species, while physical dormancy was more frequently observed among subshrubs.

Our results suggest that seed dormancy and germination traits are correlated with other aspects of seed ecology, such as dispersal season and syndrome, but not with growth form and seed mass. These is consistent with other studies in which regeneration traits varied independently from key aspects of vegetative strategies (Leishman & Westoby 1992, Grime et al. 1997, Craine et al. 2012, Hoyle et al. 2015) and studies showing a broad overlap of seed mass between dormant and non-dormant species (Jurado & Flores 2005, Norden et al. 2009, Wyse & Dickie 2017).

Our results show that in both open and closed savannas, the percentage of dormant species is relatively low (<50%) and that most species dispersed their seeds during the rainy season. These results sharply contrast the results from Baskin & Baskin (2014), in which dormancy is a prevalent functional trait in all vegetation types worldwide. Thus, our results support the hypothesis that, in seasonal environments, fruiting peaks have evolved to synchronize seed release with favorable conditions for seedling establishment (Frankie et al. 1974, van Schaik et al. 1993, Bhat & Murali 2001, Escobar et al. 2018). It also indicates that regardless the type of savanna, the timing of seed germination is controlled by both dormancy and dispersal season. Previous studies with a restrict set of species indicate that the synchronization of seed dispersal with the favorable season for germination is a key mechanism for Cerrado species to face seasonality (Salazar et al. 2011, Ramos et al. 2017). In fact, Cerrado species show lowest percent of dormancy among seasonal vegetations (Baskin & Baskin 2014).

Plant species from both habitat types may respond similarly to seasonality, given the proportion of dormant species among habitat types is similar. However, dormancy is selected as a mechanism to face not only seasonality, but also environmental uncertainty (Baskin & Baskin 2014). As disturbance frequency is greater in open environments, the proportion of dormant species is also expected to be greater. Nonetheless, in open savanna, two alternative strategies to face environmental heterogeneity seem to be equally selected: (1) spatial dispersal of seeds, represented by anemochory, and (2) temporal dispersal of germination through dormancy, represented by autochory (80% of autochorous species are dormant). Hence, 46% of species from open savanna are anemochorous and show a colonizing strategy (*sensu* Venable & Brown 1988): production of large amounts of light seeds that have wide spatial dispersal and fast and synchronized germination (Camargo 2008, Thomson et al. 2011, see Chapter 2 of this thesis). On the other hand, 40% of species from open savanna are autochorous and produce large dormant seeds that have short spatial dispersal and face environmental heterogeneity by distributing seed germination throughout the rainy season (see Chapter 2). Moreover, dormancy should have a relevant role in the recruitment of autochorous species since delayed germination might decrease competition between sibling seedlings (Ramos et al. 2017).

The low percentage of dormant species (43%) in open savannas is explained by the similar proportion of anemochorous species (non-dormant) and autochorous species (dormant). Contrarily, species from closed savannas, where disturbance frequencies are lower, face environmental heterogeneity mainly by spatial dispersal (>65% of species are endozoochorous and 20% are anemochorous). Thus, the greater diversity of strategies used to face environmental heterogeneity in open savanna agrees with what has been proposed by Grime (2006): greater disturbance frequencies leads to a differentiation of regenerative traits.

Open and closed savannas different in proportion of growth forms, dispersal syndrome, and seed mass. Endozoochory prevailed in closed savannas, while anemochory and autochory in open savannas. Endozoochory in closed savannas is related to greater seed mass, which increases the chances of seedling establishment in sites were light availability is low (Leishman et al. 2000, Moles & Westoby 2004). Additionally, the complex structure of closed savannas favors the contrast between fruits and vegetation and its location by frugivores, mainly birds (Camargo et al. 2013), and may limit wind flow and, consequently, wind dispersal (anemochory). In open habitats, anemochory is favored by the greater wind flow, while autochory is seen as a mean to increase fecundity in environments with limited resources at the expense of spatial dispersal capacity (Gottsberger & Silberbauer-Gottsberger 2006, Munhoz & Felfili 2007, Kuhlmann & Ribeiro 2016). Finally, exozoochory is the least common dispersal syndrome found in Cerrado and it occurs in open habitats, where animal movement is primarily horizontal, increasing the efficiency of this syndrome (Gottsberger & Silberbauer-Gottsberger 2006, Kuhlmann & Ribeiro 2016). The difference in seed mass between habitat types is associated to differences in the proportion of dispersal syndromes (seed mass of zoochorous species > autochorous > anemochorous) and growth forms, as seed mass increases with plant height (Moles et al. 2005).

In conclusion, open and closed savannas show similar macroclimatic conditions and in both habitat types, species respond to seasonality by synchronizing seed dispersal with the period favorable for seedling establishment or by delaying germination (via dormancy) to when environmental conditions are favorable for seedling establishment. On the other hand, dispersal syndrome, growth form, and seed mass are associated with microclimatic and soil differences. Thus, the greater disturbance frequencies and water deficits, and the lower nutrient availability of open savannas would limit the establishment of tree and shrub species, favoring two contrasting strategies to face the high environmental heterogeneity: a colonizing strategy represented by anemochorous species and a local maintenance strategy represented by autochorous species. On the other hand, in closed savannas, the lower water deficits and disturbance frequencies allow tree and shrub species to establish and develop, increasing the structural complexity and number of shaded sites in these environments, which favors endo-zoochory dispersal and large seeds. The concentration of seed dispersal during the rainy season in both habitats, the codominance of anemochorous and autochorous species in open savannas, and thee dominance of endozoochorous species in closed savannas explain the low percentage of dormant species found in both habitats.

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SUPPLEMENTARY DATA

Table S1. List of species sampled for the germination tests at two Cerrado savanna areas: the private Fazenda Botelho and the São Paulo Ecological Station Estação Ecológica de Itirapina located in Itirapina, south-eastern Brazil (22° 13’ to 22° 10’S; 47° 55’ to 47° 51’W). List ordered by family and species name, and the respective ecological and experimental information: habitat (closed and open savanna) of seed collection, fruiting peak date (see Materials and methods section for calculations), growth form (tree, shrub, subshrub and herb), dispersal syndrome (zoochory, anemochory, autochory), dispersal season (Rainy= November to March; Rainy-to-dry transition= April; Dry= May to August; Dry-to-rainy transition = September to October). Dormancy (ND = non-dormant; D = Dormant). Temperatures of the germination experiments, which were set up according to seed availability and germination percentage in optimal germination temperature (%G). Herb growth form includes grass and forbs.

Family	Species	Habitat	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)
Annonaceae	*Xylopia aromatica*	Closed	April	Tree	Endozoochory	D	Rainy-to-dry	25
Araliaceae	*Schefflera vinosa*	Closed	September	Shrub	Endozoochory	D	Dry-to-rainy	15; 20; 25; 30; 35
Asteraceae	*Chromolaena squalida*	Open	June	Subshrub	Anemochory	ND	Dry	15;20;25;30;35;20/30
Asteraceae	*Vernonanthura* sp.	Open	July	Subshrub	Anemochory	D	Dry	20;25;30;20/30
Asteraceae	*Elephantopus biflorus*	Open	August	Subshrub	Exozoochory	ND	Dry	15;20;25;30;35;20/30
Asteraceae	*Moquiniastrum barrosoae*	Open	September	Shrub	Anemochory	ND	Dry-to-rainy	15;20;25;30;35;20/30
Asteraceae	*Erechtites valerianifolius*	Open	October	Herb	Anemochory	ND	Dry-to-rainy	15;20;25;30;35;20/30
Asteraceae	*Orthopappus angustifolius*	Open	January	Subshrub	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Asteraceae	*Aldama arenaria*	Open	February	Subshrub	Exozoochory	D	Rainy	15;20;25;30;35;20/30
Bignoniaceae	*Jacaranda caroba*	Open	November	Shrub	Anemochory	ND	Rainy	20;25;30
Bromeliaceae	*Ananas ananassoides*	Closed	March	Herb	Endozoochory	D	Rainy	15; 20; 25; 30; 35
Bromeliaceae	*Dyckia* sp.	Open	January	Herb	Anemochory	ND	Rainy	25;30
Calophyllaceae	*Kielmeyera coriacea*	Closed	September	Shrub	Anemochory	ND	Dry-to-rainy	20; 25; 30
Cyperaceae	*Rhynchospora globosa*	Open	June	Herb	Autochory	D	Dry	20;25;30;35;20/30

Family	Species	Habitat	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)
Cyperaceae	*Rhynchospora rugosa*	Open	June	Herb	Autochory	D	Dry	20;25;30;35;20/30
Eriocaulaceae	*Syngonanthus nitens*	Open	August	Herb	Anemochory	D	Dry	20;25;30;20/30
Erythroxylaceae	*Erythroxylum cuneifolium*	Closed	November	Shrub	Endozoochory	ND	Rainy	25; 30
Fabaceae	*Anadenanthera peregrina var. falcata*	Closed	September	Tree	Autochory	ND	Dry-to-rainy	15; 20; 25; 30; 35
Fabaceae	*Chamaecrista langsdorffii*	Closed	April	Subshrub	Autochory	D	Rainy-to-dry	15; 20; 25; 30; 35
Fabaceae	*Dalbergia misculobium*	Closed	August	Tree	Anemochory	ND	Dry	25
Fabaceae	*Dimorphandra mollis*	Closed	June	Tree	Autochory	D	Dry	15; 20; 25; 30; 35
Fabaceae	*Machaerium acutifolium*	Closed	August	Tree	Anemochory	ND	Dry	20; 25; 30
Fabaceae	*Mimosa sommians*	Closed	April	Herb	Autochory	D	Rainy-to-dry	25
Fabaceae	*Plathymenia reticulata*	Closed	August	Tree	Anemochory	D	Dry	15; 20; 25; 30; 35
Fabaceae	*Stryphnodendron rotundifolium*	Closed	August	Tree	Autochory	D	Dry	15; 20; 25; 30; 35
Fabaceae	*Chamaecrista desvauxii*	Open	January	Subshrub	Autochory	ND	Rainy	15;20;25;30;35;20/30
Fabaceae	*Crotalaria lanceolata*	Open	January	Subshrub	Autochory	D	Rainy	15;20;25;30;35;20/30
Fabaceae	*Crotalaria incana*	Open	January	Subshrub	Autochory	D	Rainy	15;20;25;30;35;20/30
Fabaceae	*Chamaecrista cathartica*	Open	January	Subshrub	Autochory	D	Rainy	25
Fabaceae	*Mimosa xanthocentra*	Open	January	Subshrub	Autochory	D	Rainy	15;20;25;30;35;20/30
Fabaceae	*Zornia latifolia*	Open	February	Herb	Exozoochory	D	Rainy	25;30;20/30
Fabaceae	*Crotalaria* sp.	Open	April	Subshrub	Autochory	D	Rainy-to-dry	25;30
Fabaceae	*Bauhinia rufa*	Open	June	Tree	Autochory	ND	Dry	15;20;25;30;35;20/30
Fabaceae	*Senna rugosa*	Open	June	Subshrub	Autochory	D	Dry	25;30;20/30
Fabaeceae	*Stylosanthes gracilis*	Open	March	Herb	Exozoochory	D	Rainy	25
Lamiaceae	*Hyptis campestris*	Open	June	Subshrub	Autochory	D	Dry	20;25;30;35;20/30
Lamiaceae	*Hyptis caespitosa*	Open	October	Subshrub	Autochory	ND	Dry-to-rainy	15;20;25;30;35;20/30
Lamiaceae	*Hyptis pulchella*	Open	March	Herb	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Lauraceae	*Ocotea pulchella*	Closed	October	Tree	Endozoochory	ND	Dry-to-rainy	25

Family	Species	Habitat	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)
Loganiaceae	*Strychnos* sp.	Closed	October	Shrub	Endozoochory	D	Dry-to-rainy	20; 25; 30
Malpighiaceae	*Byrsonima intermedia*	Closed	February	Shrub	Endozoochory	D	Rainy	25
Malvaceae	*Sida* sp.	Open	July	Herb	Autochory	D	Dry	20;25;30;35;20/30
Malvaceae	*Byttneria sagittifolia*	Open	January	Subshrub	Autochory	D	Rainy	25
Melastomataceae	*Leandra solenifera*	Closed	December	Shrub	Endozoochory	ND	Rainy	20; 25; 30
Melastomataceae	*Miconia albicans*	Closed	December	Shrub	Endozoochory	ND	Rainy	20; 25; 30
Melastomataceae	*Miconia fallax*	Closed	November	Shrub	Endozoochory	ND	Rainy	20; 25; 30
Melastomataceae	*Miconia ligustroides*	Closed	March	Tree	Endozoochory	ND	Rainy	20; 25; 30
Melastomataceae	*Miconia rubiginosa*	Closed	March	Tree	Endozoochory	ND	Rainy	20; 25; 30
Melastomataceae	*Tibouchina* sp.	Open	August	Subshrub	Anemochory	ND	Dry	20;25;30;20/30
Melastomataceae	*Pleroma stenocarpum*	Open	August	Tree	Anemochory	ND	Dry	20;25;30;20/30
Melastomataceae	*Microlicia polystemma*	Open	August	Subshrub	Anemochory	ND	Dry	20;25;30;20/30
Melastomataceae	*Cambessedesia hilariana*	Open	December	Subshrub	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Melastomataceae	*Miconia chamisois*	Open	September	Shrub	Endozoochory	ND	Dry-to-rainy	20, 25, 30
Myristicaceae	*Virola sebifera*	Closed	October	Tree	Endozoochory	D	Dry-to-rainy	15; 20; 25; 30; 35
Myrtaceae	*Myrcia guianensis*	Closed	November	Tree	Endozoochory	ND	Rainy	15; 20; 25; 30; 35
Myrtaceae	*Myrcia splendens*	Closed	January	Tree	Endozoochory	ND	Rainy	25
Myrtaceae	*Campomanesia pubecens*	Open	November	Shrub	Endozoochory	ND	Rainy	15;20;25;30;35;20/30
Myrtaceae	*Eugenia pyriformis*	Open	November	Tree	Endozoochory	ND	Rainy	25
Poaceae	*Aristida megapotamica*	Open	June	Herb	Autochory	D	Dry	20;25;30;35
Poaceae	*Gymnopogon foliosus*	Open	June	Herb	Anemochory	ND	Dry	20;25;30;35;20/30
Poaceae	*Andropogon leucostachyus*	Open	November	Herb	Anemochory	ND	Rainy	20;25;30
Poaceae	*Sporobolus aeneus*	Open	November	Herb	Autochory	ND	Rainy	15;20;25;30;35;20/30
Poaceae	*Melinis repens*	Open	November	Herb	Anemochory	D	Rainy	20;25;30;20/30
Poaceae	*Andropogon bicornis*	Open	February	Herb	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Poaceae	*Digitaria insularis*	Open	February	Herb	Anemochory	ND	Rainy	15;20;25;30;35;20/30

Family	Species	Habitat	Fruit pick	Growth form	Dispersal syndrome	Dormancy	Dispersal season	Temperature (°C)
Poaceae	*Eustachys distichophylla*	Open	February	Herb	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Poaceae	*Loudetiopsis chrysothrix*	Open	March	Herb	Autochory	ND	Rainy	15;20;25;30;35;20/30
Poaceae	*Tristachya leiostachya*	Open	March	Herb	Autochory	D	Rainy	25
Poaceae	*Aristida riparia*	Open	April	Herb	Autochory	ND	Rainy-to-dry	15;20;25;30;35;20/30
Primulaceae	*Myrsine guianensis*	Closed	November	Tree	Endozoochory	D	Rainy	15; 20; 25; 30; 35
Rubiaceae	*Amaioua guianensis*	Closed	June	Tree	Endozoochory	ND	Dry	15; 20; 25; 30; 35
Rubiaceae	*Palicourea rigida*	Closed	March	Shrub	Endozoochory	D	Rainy	25
Rubiaceae	*Psychotria hoffmannseggiana*	Closed	April	Herb	Endozoochory	D	Rainy-to-dry	15; 20; 25; 30; 35
Rubiaceae	*Coccocypselum* sp.	Closed	April	Herb	Endozoochory	D	Rainy-to-dry	15; 20; 25; 30; 35
Rubiaceae	*Cordiera sessilis*	Closed	February	Tree	Endozoochory	ND	Rainy	15; 20; 25; 30; 35; 20/30
Siparunaceae	*Siparuna guainensis*	Closed	February	Shrub	Endozoochory	D	Rainy	25
Solanaceae	*Schwenckia americana var. hirta*	Open	November	Herb	Anemochory	ND	Rainy	15;20;25;30;35;20/30
Vochysiaceae	*Qualea dichotoma*	Closed	July	Tree	Anemochory	ND	Dry	20; 25; 30
Vochysiaceae	*Qualea grandiflora*	Closed	September	Tree	Anemochory	ND	Dry-to-rainy	15; 20; 25; 30; 35
Vochysiaceae	*Vochysia tucanorum*	Closed	September	Tree	Anemochory	ND	Dry-to-rainy	20; 25; 30
Xyridaceae	*Xyris* sp1.	Open	June	Herb	Anemochory	ND	Dry	20;25;30;35;20/30
Xyridaceae	*Xyris* sp2.	Open	June	Herb	Anemochory	D	Dry	15;20;25;30;35;20/30

CONCLUSÃO GERAL

Nossos resultados indicam que as espécies do cerrado, apesar de frutificarem ao longo de todo o ano, germinam sazonalmente no começo da estação chuvosa, como é esperado para ecossistemas sazonalmente secos (Garwood, 1983; Veenendaal et al., 1996; Marod et al., 2002; Blakesley et al., 2002, Salazar et al., 2011). Estes resultados, reforçam a ideia de que a sincronização da germinação no começo da estação chuvosa é uma característica favorecida pela seleção natural ao longo de ecossistemas sazonais, independente de grupo filogenético, forma de crescimento, síndrome de dispersão ou grau de sazonalidade do ambiente. A germinação no início da estação chuvosa deve promover uma série de vantagens evolutivas, dentre elas o aumento da estação de crescimento que permite o desenvolvimento do sistema radicular ou o acúmulo de reservas que garantem a sobrevivência na estação seca seguinte.

Nesta tese demostramos que a dormência é uma característica adaptativa no cerrado, já que incrementa as chances de estabelecimento das plântulas ao sincronizar a germinação com o início da estação chuvosa e distribuir o risco de recrutamento das espécies com capacidade limitada de dispersão espacial (i.e., autocóricas). A dormência está correlacionada evolutivamente com a dispersão espacial, mas não com o peso das sementes ou a fenologia da dispersão, e indica um *trade-off* entre a dispersão espacial e temporal das sementes. A dormência e a modulação do nicho de germinação são mecanismos alternativos de enfrentar a sazonalidade climática, e a importância relativa destes mecanismos varia com a estação de dispersão. Desta forma, a dormência pode ser uma das chaves para entender a grande diversidade vegetal do cerrado, não só porque incrementa as chances de estabelecimento das plântulas, mas também porque provavelmente permite o recrutamento de espécies autocóricas em sítios desfavoráveis para o estabelecimento das plântulas de espécies zoocóricas e anemocóricas, o que contribuiria à coexistência das espécies.

Diferente do esperado, nossos resultados mostram que a dormência e o comportamento germinativo não diferirem entre savanas abertas e fechadas, que apresentam diferentes condições ecológicas e imprevisibilidade ambiental. Isso indica que a sazonalidade climática é um filtro forte para a germinação e estabelecimento das plântulas ao longo das vegetações do cerrado, e que as espécies respondem à sazonalidade climática de forma similar independentemente do habitat. Desta forma, em ambos os tipos de vegetação a porcentagem de espécies dormentes é relativamente baixa (<50%) e a maioria das espécies dispersaram sementes na estação chuvosa. Estes resultados contrastam marcadamente com os de Baskin & Baskin (2014) que demonstram que a dormência é um traço funcional prevalente em todas as vegetações do Mundo. Este resultado reforça a hipótese de que em ambientes sazonais a seleção natural tem favorecido a sincronia da dispersão das sementes com as condições favoráveis para o estabelecimento das plântulas (Frankie et al. 1974; van Schaik et al. 1993; Bhat & Murali, 2001).

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