REFERENCE
Evolution of seed dispersal in the Cerrado biome: ecological and phylogenetic considerations

Marcelo Kuhlmann1* and José Felipe Ribeiro2

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ABSTRACT
The investigation of the phylogeny of a group of organisms has the potential to identify ecological and evolutionary processes that have been occurring within a community. Seed dispersal is a key process in the life cycle of vegetation and reflects different reproductive strategies of plants to a set of ecological and evolutionary factors. Knowing the dispersal syndromes and fruits types of a plant community may help elucidate plant-animal interactions and colonization strategies of plants. We investigated dispersal syndromes and fruit types in Cerrado formations as a parameter for understanding the evolution of angiosperm reproductive strategies in this mega-diverse tropical biome. To do this we identified and mapped the distribution of different parameters associated with seed dispersal on a phylogeny of Cerrado angiosperms genera and tested the presence of phylogenetic signal. The results showed that there were strong relationships between fruit types, seed dispersal strategies and vegetation life forms and that these traits were closely related to angiosperms phylogeny and, together, contribute to the evolution of plants in the forest, savanna and grassland formations of the Cerrado biome.

Keywords: dispersal strategies, forest, fruit types, grassland, life forms, phylogeny, savanna

Introduction
The evolution of angiosperms started about 130 million years ago (Crane et al. 1995) and, to date, there is an extraordinary diversity of its fruits, with almost a hundred morphological types being described (Spjut 1994; Eriksson et al. 2000). The appearance of fruits was a remarkable innovation in the evolutionary history of plants, which contributed greatly to the increase in seed dispersal efficiency (Pijl 1982; Fleming & Kress 2013). Understanding how the diversification of fruits and the different seed dispersal strategies are related with the phylogeny of plants of a biome is important to assess evolutionary mechanisms acting in this key process of the life cycle of vegetation (Howe & Smallwood 1982; Fleming 1991; Jordano et al. 2006). Plant-animal interactions have had central role on the evolution and diversification of fruit morphology and seed dispersal in the life of angiosperms (Jordano 1995; Fleming & Kress 2013). The changes in the structure of vegetation during the history of Earth, with the increase of forest ecosystems, allowed intense radiation of fruit types and shifts in seed dispersal patterns (Eriksson et al. 2000; Eriksson 2008). The dispersal modes associated with the strata of vegetation and the kinds of environments directly influence the dispersive capacity and geographic distribution of plant species (Fenner 1985; Lorts et al. 2008). By knowing the dispersal syndromes and the morphological patterns of the fruits of a plant community may help to elucidate

1 Instituto de Ciências Biológicas, Universidade de Brasília, Campus Universitário Darcy Ribeiro, Asa Norte, 70910-900, Brasília, DF, Brazil
2 Embrapa Cerrados, BR 020 Km 18, 73310-970, Planaltina, DF, Brazil
* Corresponding author: biomakp@gmail.com
various issues on plant-animal interactions and on different colonization strategies of plants in the environments (Howe & Westley 1997; Galetti et al. 2006; Wiesbauer et al. 2008).

Communities are built from groups of species that share certain similarities, both ecological and phyllogenetic (Blondel 2003; Cavender-Bares et al. 2009), and by grouping organisms with similar survival strategies allows to relate processes that have been playing in the evolutionary history of these groups (May & Seger 1986; Metzger 2000). Grouping plants from a community into functional groups according to their dispersal syndromes can help to understand some of these processes, since the morphology of the dispersal units generally reflect different strategies of plants for dispersion by various means, in response to a set of ecological and evolutionary factors (Thomson et al. 2010; Fleming & Kress 2013).

Since species are phylogenetically related, their morphological features are not fully independent, and can be measured statistically by calculating the “phylogenetic signal” (Revell et al. 2008). This signal can be defined as the tendency of closely related species to resemble each other more than with other species of the phylogeny at random (Blomberg et al. 2003; Losos 2008). When the phylogenetic relationship of a group of organisms of a community is known, it is possible to investigate questions, such as how strongly certain morphological and ecological characteristics are related to each other, and if they form niches or groups strongly linked throughout phylogeny (Mouquet et al. 2012; Münkemüller et al. 2012). The investigation of the phylogeny of a group of organisms, through how the conservatism of phylogenetic niche shapes the species composition of a region, has the potential to rebuild transitions in the set of organisms and identify factors driving these processes (Hawkins 2006; Pennington et al. 2006a; Crisp et al. 2009). However, it is still unknown the extent to which this trend of retaining certain morphological and ecological ancestry features has influenced the composition and diversification of species in mega-diverse biomes such as Cerrado (Simon et al. 2009).

Cerrado is a seasonal tropical ecosystem, occupying an area of over 2 million km² in South America (Klink & Machado 2005) and is one of the world’s hotspots (Myers et al. 2000), with over 12,000 species of vascular plants and 40% of endemism (Mendonça et al. 2008). It is estimated that this biome originated 10 million years ago, with the diversification of lineages of plants coinciding with the expansion of savanna vegetation around the world (Pennington et al. 2006b; Simon et al. 2009). The Cerrado biome is a vegetation complex that has different phytophysiognomies, grouped into three main formations: forests, savannas and grasslands (Ribeiro & Walter 2008). In each of these formations prevails flora species with different life forms, reproduction and growth strategies, and the distribution of the vegetation is conditioned by many environmental factors (Eiten 1994; Ratter et al. 1997), such as the depth of the groundwater, the types of soils (Haridasan 1994; Reatto et al. 2008) and frequency of fires (Coutinho 1990; Hoffmann 1996). However, little is known about the influence of different seed dispersal strategies in floristic constitution and evolution of the Cerrado formations.

Herein, we investigated the distribution of different dispersal syndromes and fruit types in the Cerrado formations, as a parameter to understand the evolution of angiosperm reproductive strategies in the biome. More specifically, we have identified and mapped the distribution of different parameters associated with seed dispersal along the phylogeny of the Cerrado angiosperms to test the presence of phylogenetic signal on these parameters. The following questions were asked: (i) What fruit types and dispersal syndromes are present in different strata and formations of the Cerrado biome? (ii) What is the distribution of the fruit types and dispersal syndromes between the Cerrado angiosperms? (iii) Are those parameters associated with seed dispersal strongly linked to angiosperms phylogeny or are they evolutionarily labile? We also discuss, based on literature, what ecological processes may have occurred during the evolution of different fruit types and seed dispersal strategies to help understand these mechanisms in the Cerrado biome.

Materials and Methods

Study area

To help us answer the questions we worked with the species of the Flora of Federal District, a region that has the most well-known and collected flora in the Cerrado (Cavalcanti & Ramos 2001; Felfili et al. 2004), which is pretty representative of the formations and vegetation types (Walter 2001) and the species that characterize the biome (Pereira et al. 1993; Ramos 1995; Proença et al. 2001). The Federal District is located in the central area of the distribution of the Brazilian Cerrado (15°30’-16°03’S and 47°18’-48°17’W), with an area of 5,810 km² and average altitude of 1,100m (Fig. 1). The region has a seasonal tropical climate, with wet (October-March) and dry (April-September) seasons, and the mean temperture varies between 12°C and 29°C (Silva et al. 2008).

Species classification

To get an overview of seed dispersal in the Cerrado, all angiosperm genera (1,500) of the biome were organized according to their syndromes, which were classified according to their primary morphological traits in three types: zoochory, anemochory and autochory (Fig. 2). To get more specific data, we worked with the better known flora of the Cerrado region, the Federal District flora. The updated lists of Cerrado genera and the species of this regional flora
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Figure 1. Map of Federal District (A) and Cerrado biome (B) (Source: Sano (2013) (A) and Ribeiro & Walter (2008) (B)).

of the Federal District were obtained on the Flora of Brazil website (Forzza et al. 2015), where 3,200 native plant species were found, distributed in 900 genera, 150 families and 43 orders (APG III 2009), corresponding to almost 30% of species, 60% of the genera and, most importantly, 85% of families described for the entire biome. The 3,200 plant species of Federal District flora were classified according to fruit types (as described in Barroso et al. 1999), dispersal syndromes (Howe & Smallwood 1982), life forms (Mendonça et al. 2008) and vegetation formations of Cerrado (forest, savanna and grassland) (Ribeiro & Walter 2008). Life forms were grouped in four strata: trees, shrubs, herbs and “vines”, in which we put together plants that “grow over other plants” such as lianas, epiphytes and mistletoes, to facilitate analysis (Fenner 1985; Lorts et al. 2008). Fruit types were grouped in eight major types: capsule (dry, dehiscent), follicle (dry, dehiscent, unicarpelar), achene (dry, indehiscent), samara (dry, winged), berry (fleshy, without stone), drupe (fleshy, with stone), schizocarp (dry, segregating into smaller units) and arthrocarp (dry, unicarpelar, segregating into smaller units) (Fig. 2).

Data analysis

To compare the proportions and relationships among the measured variables (fruit types, dispersal syndromes, life forms, vegetation formations) between the 3,200 species from the studied area, we used the G-test, using the package “DescTools” on R program and a significance level of 5%. This test was suitable for comparing the proportions and served to verify if the observed differences between the analyzed variables were significant or not (McDonald 2014).

To measure and test if the parameters associated with seed dispersal (syndromes, fruit types, fruit traits, life forms) had phylogenetic signal we used the “lambda” method (Pagel 1999), with the statistical package “phytools” (Revell 2012) on R program (version 3.2.1). This method is based on maximum likelihood tests, considering the length of the branches of a phylogenetic tree to calculate the phylogenetic signal of categorical traits, and generates a value of “lambda” ranging on a scale from “0” to “1”, where “0” corresponds to absence of phylogenetic signal and “1” maximum phylogenetic signal of the parameters (Münkemüller et al. 2012). For this test, it was first necessary to construct a phylogenetic tree for the angiosperm genera of the Cerrado. This tree was constructed using the MEGA program (version 6.0.6), with molecular sequences data obtained on the GenBank (2015) website, where we found data for 605 of the 900 genera of Federal District flora. The chloroplast DNA nucleotides used were “rbcl” and “matk”, because they are quite frequent in GenBank for angiosperms. This tree was constructed using Maximum Likelihood analysis and testing of the “bootstrap” with 1000 replications and, from there, generated a tree in the format “newick” which was used in the R program to test the phylogenetic signal of the parameters associated with seed dispersal.
Figure 2. Examples of Cerrado fruits and syndromes. **Zoochory:** (A) capsule, with arylated seeds (*Matayba guianensis*); (B) berry (*Eugenia dysenterica*); (C) drupe (*Byronima umbellata*); (D) schizocarp, with elaiosome (*Manihot violacea*); (E) artrocarp, epizoochory (*Desmodium* sp.). **Anemochory:** (F) achene (*Asteraceae*); (G) samara (*Diplopterys pubipetala*). **Autochory:** (H) follicle (*Calliandra dysantha*). (photos: Marcelo Kuhlmann).
Results

From the 3,200 native species of Cerrado analyzed, we found that most of them were herbs (53%), followed by trees (17%), shrubs (16%) and “vines” (14%). Many species occurred in more than one formation, being 58% in forests, 40% in savannas and 56% in grasslands. These proportions are similar to those found for the entire biome (Mendonça et al. 2008), confirming the good representation of the flora analyzed. The proportion of taxa between the dispersal syndromes was quite similar, featuring a 1:1:1 ratio to zoochory, anemochory and autochory, both for the 3,200 species and for the 1,500 genus analyzed of the Cerrado biome.

Concerning the eight types of fruit in the studied area, capsule was the most common (36%), followed by achene (25%), berry (11%), drupe (9%), follicle (6%), artrocarp (5%), schizocarp (5%) and samara (4%). The dispersal syndromes differed significantly according to the proportion of fruit types ($G = 2531, P < 0.0001$). Zoochory showed greater variation in types of fruits, appearing in seven of the eight categories. “Dry fruits” together (excluding berry and drupe) represented 80% of the species and genera also of the flora analysed. Several traits were found in fruits related to each of the syndromes and some families were more strongly linked to each syndrome based on their number and proportion of species and genera (Tab. 1).

The proportion and number of species of each dispersal syndrome in the studied area varied significantly between the vegetation formations ($G = 187, P < 0.0001$) and between life forms of vegetation ($G = 847, P < 0.0001$). Forests had higher proportion of zoochory (43%), while autochory predominated on savannas (39%) and grasslands (44%). Among the life forms, tree and shrub (woody) had higher proportion of zoochory (71% and 50% resp.), herbs had the highest proportion of autochory (50%) and among “vines” anemochory predominated (58%). Relating the

Table 1: Fruit types, traits, and most representative families for each dispersal syndrome for 3,200 species and 150 families of the Cerrado. The number of species is between parentheses.

<table>
<thead>
<tr>
<th>Syndromes</th>
<th>Fruit types</th>
<th>Fruit traits</th>
<th>Most representative families</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zoochory</td>
<td>berry (355)</td>
<td>fleshy (628)</td>
<td>Rubiaceae (79)</td>
</tr>
<tr>
<td></td>
<td>drupe (273)</td>
<td>adherent (135)</td>
<td>Myrtaceae (75)</td>
</tr>
<tr>
<td></td>
<td>achene (184)</td>
<td>elaiosome (117)</td>
<td>Euphorbiaceae (49)</td>
</tr>
<tr>
<td></td>
<td>capsule (129)</td>
<td>aril (113)</td>
<td>Solanaceae (35)</td>
</tr>
<tr>
<td></td>
<td>schizocarp (54)</td>
<td>pseudo fruit (36)</td>
<td>Lauraceae (24)</td>
</tr>
<tr>
<td></td>
<td>artrocarp (44)</td>
<td>resin (26)</td>
<td>Moraceae (19)</td>
</tr>
<tr>
<td></td>
<td>follicle (41)</td>
<td>mimetic seed (25)</td>
<td>Annonaceae (17)</td>
</tr>
<tr>
<td>Anemochory</td>
<td>capsule (577)</td>
<td>plumes (412)</td>
<td>Asteraceae (290)</td>
</tr>
<tr>
<td></td>
<td>achene (328)</td>
<td>winged (343)</td>
<td>Orchidaceae (250)</td>
</tr>
<tr>
<td></td>
<td>samara (115)</td>
<td>lightness (277)</td>
<td>Apocynaceae (91)</td>
</tr>
<tr>
<td></td>
<td>schizocarp (7)</td>
<td></td>
<td>Bignoniaceae (84)</td>
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<td></td>
<td>follicle (5)</td>
<td></td>
<td>Malpighiaceae (70)</td>
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<tr>
<td>Autochory</td>
<td>capsule (436)</td>
<td></td>
<td>Dioscoreaceae (27)</td>
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<td></td>
<td>achene (293)</td>
<td></td>
<td>Bromeliaceae (22)</td>
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<tr>
<td></td>
<td>follicle (160)</td>
<td></td>
<td>Ericaceae (19)</td>
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<tr>
<td></td>
<td>artrocarp (112)</td>
<td></td>
<td>Vochysiaceae (14)</td>
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<td></td>
<td>schizocarp (87)</td>
<td></td>
<td>Aristolochiaceae (8)</td>
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<tr>
<td></td>
<td>“not evident” (928)</td>
<td></td>
<td>Fabaceae (209)</td>
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<tr>
<td></td>
<td>explosive fruits (160)</td>
<td></td>
<td>Cyperaceae (121)</td>
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<td></td>
<td>Convulpulaceae (69)</td>
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<td>Lamiaceae (65)</td>
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<td>Melastomataceae (33)</td>
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<td>Malvaceae (32)</td>
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<td>Acanthaceae (30)</td>
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<td>Verbenaceae (25)</td>
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<td></td>
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<td></td>
<td>Amaranthaceae (23)</td>
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<td></td>
<td></td>
<td></td>
<td>Gentianaceae (18)</td>
</tr>
</tbody>
</table>
three variables together (dispersal syndrome, life form and vegetation formation), it was observed that the syndromes showed similar ratios among the three formations in all four strata of vegetation (Fig. 3). Regardless of the Cerrado formations, zoochory was always more associated with the woody strata (tree and shrub), while autochory was more associated with herbs and anemochory showed higher proportion related to "vines".

The types of fruits and dispersal syndromes of the studied species differed significantly in the proportion of families in which they occurred within the five major lineages of angiosperms \((G = 182, P < 0.0001\) and \(G = 66, P < 0.0001\) respectively). With monocots only four types of fruits were found (capsule, drupe, berry, achene) and only among the rosids did all eight kinds of fruits occur. Capsule was presented in 80 families (53%) and the artrocarps in only two (1%) (Fabaceae e Lamiaceae). Dry fruits occurred in 125 families (83%) and flesh fruits in 81 families (55%). Zoochory was presented in 100 of the 150 families (67%), autochory in 62 (41%) and anemochory in 41 (27%). Of the total families, 110 were associated exclusively to only one of the syndromes, while in the other 40 there was more than one dispersal mode. Zoochory was the one with the largest number of exclusive families (63), followed by autochory (34) and anemochory (13) (Fig. 4).

The test for phylogenetic signal resulted in a significant and high value of "lambda" (close to 1) for all parameters associated with the dispersal strategies (Tab. 2). This indicates that these parameters are strongly associated with the phylogeny of angiosperms. Mapping the chosen parameters in the Cerrado angiosperms phylogeny, at a genus level, indicated a phylogenetic signal, showing that the dispersal syndromes were distributed non-randomly in the phylogenetic tree, forming well defined phylogenetic niches between the branches of the phylogeny (Fig. 5). The distribution of the other parameters analyzed (fruit type, fruit dry/fleshy, fruit traits and life forms) should show similar patterns, forming well defined niches throughout the phylogeny.

Figure 3. Comparison of the dispersal syndromes among different life forms in forest, savanna and grassland for 3,200 species of the Cerrado.

Figure 4. Proportions in a sample of 150 Cerrado angiosperms families that have each dispersal syndrome in major lineages of angiosperms: \(B\) \(Ang\) = basal angiosperm, \(Mon\) = monocots, \(B\) \(Eud\) = basal eudicots, \(Ros\) = rosids, \(Ast\) = Asterids. Mixed families have more than one dispersal syndrome. Number of families is indicated.

Figure 5. Phylogenetic structure and mapping of dispersal syndromes for Cerrado angiosperms genera (605 genera, 141 families), grouped in major lineages: Basal angiosperms, Monocots, Basal eudicots, Rosids and Asterids. This phylogeny is in agreement with APG III (2009). Please see the PDF version for color reference.
Table 2. Phylogenetic signal values for different parameters related to seed dispersal among Cerrado angiosperms.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Phylogenetic signal (&quot;lambda&quot;)</th>
<th>P-value</th>
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<tbody>
<tr>
<td>Dispersal syndrome</td>
<td>0.892</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fruit type</td>
<td>0.925</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fruit dry/flesh</td>
<td>0.933</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fruit traits</td>
<td>0.909</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Life form</td>
<td>0.937</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Discussion

Ecology and evolution of seed dispersal in the Cerrado biome

Dry fruits, especially capsule and achene, predominated among the species analyzed in the studied areas of Cerrado, while there was no predominance of any particular type of seed dispersal among the analysed flora or for Cerrado genera, suggesting that the three syndromes (zoochory, anemochory, autochory) are probably equally distributed (1:1:1) among all plants of the biome. However, as Cerrado is a mosaic of vegetation, these characteristics differed mostly between particular formations, with the highest proportion of zoochorous fruits and fruit-eating animals, especially birds and mammals (Bolmgren & Eriksson 2005). Finally, these hypotheses seem to describe plausible ecological processes to explain the evolution of zoochory in tropical biomes and also in Cerrado.

As one-third of the species and genera analyzed for the Cerrado presented traits related to seed dispersal by animals, the importance of fauna in evolutionary history and constitution of much of the biome vegetation is relevant, mainly between woody species and forest formations. Zoochory was the syndrome with greater variety of fruit types in the studied area, including, in addition to berries and drupes, dry fruits with various traits such as aril, elaiosome, pseudo fruits and also hooks and spines that can adhere to mammal fur or bird plumage, related to epizoochory. About 10% of the analysed zoochoric fruits had traits related to epizoochory and almost all of them were herbs that occur in grasslands, which enhances efficiency of this dispersal strategy in this environment, where ground animals move primarily horizontally (Gottsberger & Silberbauer-Gottsberger 2006). Fruits with fleshy tissues evolved many times and independently during the history of plants (Bolmgren & Eriksson 2010; Fleming & Kress 2013) and several hypotheses have been raised to explain this. First, fleshy fruits attracted frugivore animals that fed pulp and contributed to seed dispersal and also this pulp could contain substances capable of decreasing the retention time in animal intestines, reducing the harmful effects of frugivory (Herrera 1989; Cipollini & Levey 1997). The evolution of fleshy fruits was also associated consistently with the increase in seed mass (Leishman et al. 2000) and selective pressures have favored larger and thicker seeds, because they would be more resistant to mechanical and chemical abrasion of the digestive tract of animals (Bolmgren & Eriksson 2010). In addition, larger seeds have larger reserves of nutrients that allowed them to establish better in dense vegetation and low-light environments, home to most of the fruit eaters (Leishman et al. 2000; Tiffney 2004). Thus, the appearance of fleshy fruits would have favored the dispersion of large seeds, which require biotic means to transport greater distances for establishing outside the intermediation of the parent plant (Janzen 1969; Eriksson et al. 2000; Eriksson 2008). Frugivores of different sizes also would have played an important role in the selection of zoochorous fruits, since there is a positive relationship between the size of the diaspore and the size of the animal that is capable of removing the fruit (Jordano 2000; Galetti et al. 2013). In geological time, abiotic dispersal modes predominate during the Cretaceous period (130 Ma) between gymnosperms and angiosperms (Tiffney 1984), but with the extinction of dinosaurs and climate change at the beginning of the Tertiary period (65 Ma) there was greater development of forest systems with more dense vegetation, which was accompanied by greater abundance and diversity of zoochorous fruits and fruit-eating animals, especially birds and mammals (Bolmgren & Eriksson 2005). Finally, these hypotheses seem to describe plausible ecological processes to explain the evolution of zoochory in tropical biomes and also in Cerrado.

Wind dispersed species have diaspores of different sizes and extraordinary aerodynamic shapes that help them...
float to be transported far away from the parent plant (Pijl 1982). Among the anemochoric plants of Cerrado studied here, traits like plums, winged diaspores and lightness (tiny seeds as Orchidaceae) predominate. The fruit types that were more associated with wind dispersal were capsule, achene and samara (which was exclusively anemochorous). To understand the evolution of wind dispersal, some models have been proposed based on physical factors that affect the aerodynamic ability of diaspores, such as wind speed and direction and height of release (Okubo & Levin 1989; Levin et al. 2003). Different diaspores formats respond unequally to these factors, which act as selective pressures in the anemochorous fruits and seeds, since they influence the distance they are transported (Levin et al. 2003). The development of smaller and lighter seeds also favored the selection of anemochoric plants by providing greater productivity, and the environment where the individual lives is another important factor to be taken into account, since wind dispersal of the same plant species will be drastically affected if it is in a cleared area or in a dense forest (Eriksson & Jakobsson 1999). As found for the species analysed in Cerrado, anemochory showed similar proportions in all formations, being slightly higher in savanna and grasslands than it was in the forests, for trees, shrubs and herbaceous species. However, there was strong relationship of this syndrome with the “vines” strata (almost 60% of anemochory), which included plants growing over other plants such as lianas (many Apocynaceae and Bignoniaceae) and epiphytes (many Orchidaceae). These plants grow seeking for light and greater exposure to wind effect, especially in the canopy of trees in forests, indicating important strategic role of this life forms in the evolution of anemochoric plants. Although we included among “vines” plants like mistletoes, which are predominantly zoochorous, they represented less than 10% of this strata in the studied area, and this also could reinforce the predominance of anemochory among the plants that “grow over other plants”.

For autochory dry fruits such as capsule, follicule and achene predominated and schizocarps and artocarps also had higher proportions in this syndrome. Autochory was also strongly associated with herbs, which presented almost 80% of autochory in the studied area. Among the special traits for this dispersal strategy, elastic or explosive dehiscence characterized active autochory, which is favored in hot, dry periods (Gottsberger & Silberbauer-Gottsberger 2006). This trait would have evolved from the improvement of dehiscence of the pericarp tissue of some fruits (greater torsion and pressure), allowing the expulsion of seeds at longer distances (Barroso et al. 1999). But curiously, the “no evidence” of any traits associated with seed dispersal was the one that was more present in autochorous diaspores, and also accounted for almost a third of all species analyzed in this study in Cerrado. Willson et al. (1990) found that between 20 and 50% of regional floras in different parts of the world did not have special features for seed dispersal, and some explanations for this phenomenon have been raised. Possibly these diaspores are associated with secondary forms of dispersal and not directly related to their morphology, and thus required occasional dispersal agents such as rainwater or grazing animals that swallow the seeds when feeding (Vargas et al. 2012). An additional explanation for the large number of taxa without obvious attributes to seed dispersal (mainly herbaceous species) is that these special features require higher energy costs, which could reduce plant fertility (Eriksson & Jakobsson 1999). In herbaceous plants, the cost-benefit ratio between production of many small seeds versus a few large seeds (which would require special appendages to dispersal, like wings or fleshy tissues) seems to have been favored by natural selection by opting for higher fertility and productivity instead appendices for dispersal (Eriksson & Jakobsson 1999). More open environments, such as savannas and grasslands of Cerrado, where herbaceous species prevail, also favor lower energy cost dispersal modes like passive autochory, so that large seeds would have greater importance in denser and shady environments, like forests (Westoby et al. 1996). Thus, the lack of special features to seed dispersal itself would be the selected trait on these species to increase dispersal efficiency, which would respond in favor of improved productivity, being as important for seed dispersal as any morphological structure designed for this.

The results showed that there seems to be strong evolutionary relationship between life forms and dispersal strategies in flowering plants such as woody plants X zoochor, “vines” X anemochory and herbaceous plants X autochory, and the differences observed between the vegetation formations of Cerrado seem to reflect the life forms of vegetation that predominate in each environment. In addition, this can be also confirmed if analyzing phytosociological studies in Cerrado (Pinheiro & Ribeiro 2001; Fonseca & Silva,Junior 2004; Fontes & Walter 2011), in which was observed that areas with low floristic similarity between them, but with the same structure of vegetation, were quite similar in terms of dispersal strategies, both for the number of species and the number of individuals of each syndrome. Thus, it is expected that even distant communities with high floristic differences may be quite similar for functional ecological processes, as in the case of dispersal strategies, since they are similar regarding the structure of the vegetation (May & Seger 1986).

For the Cerrado biome, another possible selective pressure that can be highlighted to understand the evolution of seed dispersal in this biome is the seasonal climate (with dry and rainy season). It has been demonstrated that anemo and autochorous species produce fruits mainly in the dry season, since this period provides favorable conditions for the drying process and fruit dehiscence to release the seeds, while zoochorous species generally produce fruits during the rainy season, when fleshy fruits can keep attractive for longer time. On the other hand, dry zoochorous fruits,
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such as in *Copaifera* and *Hymenaea*, tend to produce fruits during the dry season (Batalha & Mantovani 2000; Batalha & Martins 2004; Gotsberger & Silberbauer-Gotsberger 2006). As a vegetation that is susceptible and conditioned by fire (Coutinho 1990), especially savannas and grasslands, this is another factor that can play selective pressure on fruit types in Cerrado. It has been demonstrated that fire increases nutrient cycling on soil and stimulates flowering and thus seed production in some Cerrado plants, such as Poaceae, Cyperaceae and Bromeliaceae (Munhoz & Felfili 2007), and that high temperatures caused by fire can also accelerate fruit drying and seed release and higher germinability in some species, like *Kielmeyera coriacea*, which have a coriaceous dry fruit (Cirne & Miranda 2008; Zaidan & Carreira 2008). However, there is still little information available about the fire effects on fruit production and germination of the Cerrado species, especially in woody plants (Palermo & Miranda 2012).

**Phylogenetic signal of seed dispersal parameters**

As plants have diversified throughout evolutionary history they colonize wide variety of environments and developed different life forms and seed dispersal strategies (Tiffney 1984; Eriksson et al. 2000; Moles et al. 2004; 2005). The tests in this study showed that fruit types, seed dispersal strategies and life forms of vegetation had high value of phylogenetic signal, indicating that these parameters are strongly linked to the phylogeny of Cerrado angiosperms at a genus level. Since species with genetic proximity tend to be ecologically similar (Darwin 1859; Derrickson & Ricklefs 1988), analyses of phylogenetic signal can serve to assess the extent to which phylogeny explains similarities or differences between organisms (Harvey & Pagel 1991; Münkemüller et al. 2012).

The mapping of parameters associated with seed dispersal (syndromes, fruit types and life forms) in the phylogenetic tree also enabled to visualize the formation of some phylogenetic niches, indicating that these parameters were not randomly distributed in the phylogeny and were more closely related to some taxa than others. For example, among the basal angiosperms predominated fleshy fruits and zoochorous, represented mainly between Laurales and Magnoliidae, and anemochory and winged seeds being present only in Aristolochiaceae. In monocots, composed mostly of herbaceous plants, capsular fruits and autochory predominated, but some orders and families showed a greater association with other syndromes, such as Orchidaceae with anemochory and Asimilatae, Arecales and Zingiberaceae with zoochory. Between basal eudicots zoochorous was remarkable in Cactaceae, Dilleniidae and Santalales. Between rosid zoochorous was highlighted in Myrtaceae, Cucurbitaceae, Rosales, Sapindales and Malpighiales, except the Malpighiaceae family, where anemochory and samara fruits dominated. And between asterids, phylogenetic niches for anemochory in the families Asteraceae, Apocynaceae and Bignoniaceae (which are rich in liana species), niches for zoochory in Ericales and Rubiaceae and niches for autochory in several families of herbaceous plants of the Lamiales order were observed.

Ecological parameters, such as plant dispersal strategies, combined with phylogenetic and statistic inferences of the taxa involved, consist of powerful tools for understanding evolutionary patterns and processes in a community (Pagel 1999). However, some authors recommend certain care regarding the use of phylogenies in biological studies to assess evolutionary phenomenon (Losos 2008), since the phylogeny itself could not be interpreted as a causal mechanism of the current phenotype of living beings, but only as the pattern, reflection or effect of their evolutionary history, and would serve to raise hypotheses about the mechanisms that generated this pattern (Losos 2011). In contrast, some authors consider that phylogenetic patterns in a community can also be caused by the existing niche conservatism among similar taxa (Wiens et al. 2010). Once species and clades tend to retain their niches and ancestral features, characterizing the niche conservatism (Harvey & Pagel 1991), the observation that certain ecological traits in a community are phylogenetically conserved could be interpreted both as a pattern of ecological similarity over time and as a process that helped to create this pattern in evolutionary history (Wiens et al. 2010). The presence of niche conservatism may also suggest that some ecological processes are more plausible than others, helping even to predict changes in response to environmental changes, such as climate change or species extinctions, that can cause population fragmentation in closely related clades (Knapp et al. 2008; Helmus et al. 2010).

**Final considerations**

Habitat changes occur faster than species can adapt to these changes and, currently, the destruction of natural ecosystems has been considered the greatest threat to biodiversity (Dirzo & Raven 2003; Holt & Gomulkiewicz 2004). Models of occupation and land use in Cerrado have led to loss of more than 50% of the original vegetation of the biome (Sano et al. 2008), bringing consequences such as soil degradation, increased invasive species and compromising the water cycles (Klink & Machado 2005), with the deforestation of Cerrado even affecting rainfall patterns and increasing the duration of the dry season in Amazon regions (Costa & Pires 2010). The observation that biomes are phylogenetically conserved (Crisp et al. 2009) also implies that its evolutionary potential could be seriously compromised by environmental changes, so that ecological processes such as seed dispersal, which have strong links with the angiosperms phylogeny, could be dramatically affected by the decline in biodiversity, with whole clades being affected, not just species in particular,
causing a break in the phylogeny of plants. With this in mind, and knowing the ecological requirements for the persistence of the species in a phylogenetic perspective, it is possible to predict which changes in habitat a species or clade can tolerate based on those requirements that were important to their development during evolution (Wiens et al. 2010), and this could assist recovery programs of degraded areas like that found in the Cerrado.

These considerations indicate that the environmental conditions today can have very ancient roots, and the study of phylogeny is important to understand the evolution and distribution of morphological and ecological traits among taxa, but alone it does not identify all the processes that generated such phylogenetic patterns. Cerrado has a vegetation of great antiquity and presents various climatic and soil peculiarities that determine the distribution of its flora, with a wide range of ecological processes to be investigated phylogenetically to better understand the evolution of this mega-diverse biome. Here we evaluated the seed dispersal process from an ecological and phylogenetic point of view, and found that traits such as dispersal syndromes, fruit types and life forms were closely related to each other and with phylogeny, contributing together to the evolution and survival of angiosperms and influencing the biodiversity in the forest, savanna and grassland formations of the biome.

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Marcelo Kuhlmann and José Felipe Ribeiro


