

UNIVERSIDADE FEDERAL DE MINAS GERAIS INSTITUTO DE CIÊNCIAS BIOLÓGICAS

Departamento de Botânica





## Programa de Pós-Graduação em Biologia Vegetal

## **ROBERTA DAYRELL DE LIMA CAMPOS**

# ECOLOGY AND EVOLUTION OF SEED DORMANCY IN CAMPOS RUPESTRES

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Biologia Vegetal.

Área de Concentração Fisiologia Vegetal e Ecologia

## **BELO HORIZONTE – MG**



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Orientador: Prof. Dr. Fernando Augusto de Oliveira e Silveira Universidade Federal de Minas Gerais

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#### RESUMO

Ciclos reprodutivos de plantas adultas terminam com a dispersão de sementes, enquanto o estabelecimento de seus descendentes se inicia com a germinação de sementes. A dormência regula o tempo de germinação de sementes, permitindo que cada um desses eventos da vida da planta aconteça sob condições favoráveis. Usamos um conjunto de dados na escala de comunidade para testar hipóteses de ecologia e evolução na ocorrência de dormência em sementes. Relatamos a ocorrência de dormência primária em plantas de campos rupestres, pertencentes às savanas brasileiras (cerrado). Reunimos dados originais (1) experimentais de germinação e viabilidade de 26 espécies e (2) de pesquisa bibliográfica sobre a ocorrência de dormência e viabilidade em sementes de campos rupestres. A frequência de sementes de campos rupestres dormentes foi determinada e contrastada com frequências relatadas para savanas e para todo o mundo. Examinamos os processos ecológicos e filogenéticos que conduzem a evolução da dormência das sementes. Nosso levantamento resultou em 231 populações pertencentes a 27 famílias de plantas. Frequências de ausência de dormência foram acentuadamente diferentes entre campos rupestres e savanas, e reportamos que o campo rupestre é a vegetação com a menor proporção de sementes dormentes no mundo. A análise filogenética sugeriu uma evolução convergente na ocorrência de dormência, evidenciada pela distribuição aleatória dessa característica em todos os principais clados. No entanto, nenhuma das correlações ecológicas investigadas aqui - período de dispersão de sementes, microhabitat, forma de vida ou modo de dispersão - influenciou na ocorrência de dormência. Um maior número de populações de campos rupestres dispersa sementes durante período favorável, indicando que o controle sobre o período de dispersão, e não a dormência das sementes, garante que a germinação ocorra em condições favoráveis. Relatamos também uma grande variação na viabilidade das sementes entre taxa, o que aponta para uma capacidade desigual de reprodução sexual. Peculiaridades de campos rupestres referentes aos padrões de ecologia de semente podem estar relacionadas com estabilidade geologica e infertilidade de solo desses ambientes.

Palavras-chave: ausência de dormência; campos neotropicais; cerrado; comunidade; período de dispersão de sementes; germinação de sementes.

#### ABSTRACT

Reproductive cycles of adult plants end with seed dispersal, whereas the establishment of their offspring begins with seed germination. Seed dormancy enables each of these life events to happen under favorable conditions by regulating the timing of germination. Here we used a community-level dataset to test hypotheses on the ecology and evolution of seed dormancy. We report the occurrence of primary dormancy in plants growing in campos rupestres, Neotropical grasslands of the Brazilian savanna (i.e., *cerrado*). We (1) provide original data from germination and viability experiments of 26 species and (2) surveyed the literature for information on dormancy occurrence and viability of campos rupestres seeds. Seed dormancy occurrence in campos rupestres was determined and contrasted with reported frequencies from savannas and worldwide. Ecological and phylogenetic processes driving the evolution of seed dormancy were examined. We gathered data from 231 populations of 27 plant families. Frequencies of nondormancy markedly differed among *campos rupestres* and savannas, with campos rupestres showing the lowest proportion of nondormancy across all vegetations in the world. Phylogenetic analysis suggested a convergent evolution in dormancy occurrence, as evidenced by its random distribution across all major clades. However, none of the ecological correlates investigated here – season of seed dispersal, microhabitat, life form or dispersion mode – seems to influence seed dormancy occurrence. A greater number of *campos rupestres* populations dispersed seeds during favorable period, indicating that control over timing of seed dispersal rather than seed dormancy assures germination to occur under favorable conditions. We also report a wide variation on seed viability between taxa, pointing to uneven ability for sexual reproduction. Campos rupestres peculiarities regarding patterns of seed ecology could be related to geological stability and infertile soils of these environments.

Keywords: Community assessment; Neotropical grasslands; nondormancy; seed germination; seed dispersal timing; tropical savanna.

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Antes de nós nos mesmos arvoredos Passou o vento, quando havia vento, E as folhas não falavam De outro modo do que hoje.

Passamos e agitamo-nos debalde. Não fazemos mais ruído no que existe Do que as folhas das árvores Ou os passos do vento.

Tentemos pois com abandono assíduo Entregar nosso esforço à Natureza E não querer mais vida Que a das árvores verdes.

Inutilmente parecemos grandes. Salvo nós nada pelo mundo fora Nos saúda a grandeza Nem sem querer nos serve.

Se aqui, à beira-mar, o meu indício Na areia o mar com ondas três o apaga, Que fará na alta praia Em que o mar é o Tempo?

Fernando Pessoa (Odes de Ricardo Reis)

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#### INTRODUCTION

The evolution of the seeds represented a remarkable life-history transition for plants. Seeds provided plants with large ecological and evolutionary advantages, including extended survival periods after dispersal, increased resistance to adverse environmental conditions, increased dispersal distance and, subsequently, increased gene flow (Linkies *et al.* 2010). Additionally, many seeds present a condition which regulates timing of seed germination – i.e., dormancy – enabling seeds to avoid germination during periods that are only ephemerally favorable (Linkies *et al.* 2010, Baskin & Baskin 2014). Because germination is an irreversible process, selection should favor strategies that prevent seeds from germinating under unfavorable conditions for seedling establishment, thereby reducing extinction risk (Jurado & Moles 2002).

Dormancy is expressed by physiological, morphological, and anatomical mechanisms, allowing seeds to interact with their ecological environment in several ways (Linkies *et al.* 2010). The presence of at least one of these mechanisms in seeds is more frequent than their absence, i.e., the lack of dormancy (Baskin & Baskin 2004, 2014), especially in environments with seasonal frost and/or drought (Jurado & Flores 2005, Baskin & Baskin 2014). Hypotheses test on the evolution of different kinds of seed dormancy indicated that the ability of seeds to sense and respond physiologically to the environment to regulate dormancy was present at the origin of seed plants. Nondormancy, however, was found to be a highly derived and ephemeral state, present primarily at the tips of the phylogenetic tree (Willis *et al.* 2014). Therefore, both phylogenetic constraints and environmental filters seem to play a role in the evolution of seed dormancy.

Here we report the occurrence of primary dormancy in plants growing in *campos* rupestres, Neotropical montane grasslands that belongs to the *cerrado* biome. The *Cerrado* is the most species-rich savanna in the world (Mendonça *et al.* 2008), with typical landscape consisting of a complex mosaic of savanna physiognomies on the well-drained interfluves with riparian forests along the watercourses (Ratter *et al.* 1997). The *campos rupestres* occur in shallow, acidic, nutrient-poor and excessively drained quartzite-derived or ironstone soils above 900m above sea level (Giulietti *et al.* 1997, Jacobi *et al.* 2007, Alves & Kolbek 2010), where plants often experience strong winds, high irradiance exposure, frequent fires, high daily thermal amplitudes and water shortage during dry season (Giulietti *et al.* 1997, Madeira & Fernandes 1999). These montane grasslands are geologically and geomorphologically old and stable environments (Saadi 1995), and were edaphically isolated from surrounding vegetation changes over past climatic shifts (Alves & Kolbek 1994).

Since seedlings are particularly susceptible to harsh condition (Leck *et al.* 2008), we hypothesized that seed dormancy would be a widespread strategy in *campos* rupestres, ensuring germination under favorable conditions and distributing plants offspring across time, bet-hedging against unpredictable fire events (Venable 2007, Poisot *et al.* 2011, Moreira & Pausas 2012). We further predicted that seed dormancy has evolved especially in seeds dispersed in late-rainy season, when seedlings would not have enough time to settle enough to endure the dry period (Silveira *et al.* 2012). Additionally, we considered that other ecological correlates – such as microhabitat, seed dispersal mode and plant life form – and phylogenetic relatedness could also influence seed germination strategies (Bu *et al.* 2008, Kos *et al.* 2012, Silveira *et al.* 2012).

Besides dormancy, there are other reasons why seeds may not germinate under favorable conditions (Hilhorst 2011). Many species have high proportions of

embryoless seeds or unviable embryos. These factors converge to produce exactly the same response as if seeds were dormant: the absence of germination (Silveira 2013). Since embryo presence and viability are often overlooked in germination studies, we aimed to investigate the importance of these factors in *campos rupestres* seeds.

Altogether, in this study, we have reviewed the ecology and evolution of seed dormancy in *campos rupestres*. Specifically, we (1) screened for dormant seeds among 26 species from campos rupestres in Brazil and assessed their viability; (2) searched literature for information on dormancy occurrence and viability of *campos rupestres* seeds; (3) examined the processes driving the evolution of seed dormancy; and (4) discussed the phylogenetic and biogeographical implications of our findings for the general understanding of seed dormancy and viability in *campos rupestres*.

#### **MATERIALS AND METHODS**

#### Literature search and data extraction

We conducted a comprehensive literature search using three online search services to identify experimental germination tests with seeds collected at *campo rupestre* sites (Figure 3A). We used a topic search in Web of Science, all indexes search in Scielo and a broad search at Google Scholar (cf. Appendix S1, Supporting information for search terms), which yield a total of 49, 8 and 1160 studies, respectively (on December 5th 2014). In addition, we included unpublished data of Master and PhD theses, and also articles of the present authors that were missed by our literature search or that are currently in press. We combined the results from all searches and removed duplicates.

We designated studies as relevant if several criteria in form, content and method were matched, following criteria: 1) We included peer-reviewed primary literature and grey literature (Master and PhD theses) written in English or Portuguese. Review papers were not included. 2) Studies had to perform germination experiments with fresh seeds – because dormancy cannot be safely determined in stored seeds (Baskin *et al.* 2006) – collected at *campo rupestre sensu stricto* sites in Brazil (Alves *et al.* 2014). Hence, we excluded results from stored seeds experiments or that collected seeds in a different vegetation type (e.g. altitudinal grasslands, and Cerrado typologies such as *campo limpo, campo cerrado* and *cerrado rupestre*). 3) Studies that exposed seeds to some kind of dormancy break treatment and did not present data of control group were not included. 4) We also excluded results from populations not identified at the species level.

In total, 56 studies matched our criteria, providing 180 species in 17 families (due to multiple reported species per study; Appendix S2, Supporting information). In order to increase representation of non-studied taxa, germination experiments (described further in the "Germination experiments" topic) were performed in additional 26 species belonging to 16 families (10 additional families). Thus, we were able to gather information from a total of 206 species (plus 25 subspecies, varieties or populations) belonging to 27 families. Since among population variation in seed dormancy and germination is commonplace (Anderssen & Milberg 1998, Lacerda *et al.* 2004), we considered different populations as different evolutionary units, using study location to distinguish among them.

We did not look for variation in germinability among different years of collection because germination was tested multiple times in only a few species. Thus, whenever we found information on more than one year of collection, we first considered the studies which assessed seed viability or secondly the average values of germinability of all years of collection.

For each species/population examined and any given treatment in each publication, we recorded the following information whenever available: article title, year, journal, study site (region, location and coordinates), collection date or dispersal period, dispersal mode (biotic or abiotic), life form (tree, shrub or herb), habitat (xeric, mesic or wet), experiment length (number of days), temperature and photoperiod of incubation, number of replicates and seeds per replicates, germinability (germination percentages), germination time or rate (e.g. mean germination time, mean velocity, germination rate index), embryoless seeds (percentages), viable seeds (percentages), types of used treatments in pollination or seeds (e.g. manual cross pollination, seed scarification, seed incubation with giberellic acid).Species names were updated according to Brazil Plant Species List available at Reflora (http://reflora.jbrj.gov.br) in December 2014.

#### Viability and germination experiments

Aiming to increase representation of non-studied taxa, fruits of 26 species were collected at quartzite *campos rupestres* of Santana do Riacho (MG), between August of 2013 and June of 2014. Fresh seeds extracted from fruits were immediately set to germinate into Petri dishes layered with double sheet of filter paper, and moistened with Nistatina® suspension to prevent fungi growth whenever necessary (Appendix S3, Supporting information). Seeds were placed in germination chambers kept at the constant temperature of 25°C under a 12-hr photoperiod, which have been shown to be the optimum conditions for germination of most *cerrado* species (Zaidan & Carreira 2008, Melo *et al.* 2008). All seeds were monitored for 50 consecutive days, a conservative caution regarding the 30 days parameter (Baskin *et al.* 2006) that still allowed our data to be comparable with other studies (Baskin & Baskin 2014).

Germination was checked every 24 hours and germination was determined upon radicle emergence. After the germination trials, seeds that did not germinate were cut and placed in a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC) for 48h under dark conditions in chamber at 25°C (Peters & Lanham 2005) to assess seed viability.

#### Seed viability in campos rupestres seeds

We gathered information on seed germination and viability of populations growing in *campos rupestres* to assess the percentages of empty, unviable, nondormant and dormant seeds. Only experiments that performed the tetrazolium test were included, except for Fabaceae whose scarification treatment data was also considered as viability assessment.

#### **Determination of primary dormancy class**

There are many definitions of seed dormancy. In this study, we considered seed dormancy as the failure of viable seeds to germinate, despite environmental conditions including water, temperature, light and gases are favorable for germination (Vleeshouwers *et al.* 1995, Bewley 1997, Geneve 2005, Hilhorst 2011). Due to the limited information for the majority of *campos rupestres*' species, we did not attempt to determine seed dormancy class *sensu* Baskin and Baskin (2004), but were mostly concerned about the occurrence of primary dormancy itself. Based on the criteria used by Jayasuriya *et al.* (2013), and accounting for particularities of collected data, we divided seeds into three categories: dormant (D), dormant and nondormant (D+ND) and nondormant (ND). If most (70-100%) of the viable seeds germinated in a maximum of about 4 weeks, they were considered to be nondormant. If less than 40% of viable seeds germinated during the same period, they were considered as dormant. The remaining

viable seeds that germinated 40 to 69% were considered as dormant and nondormant (Appendix S2, Supporting information). We also classified seeds which germinated only over a narrow range of physical conditions as conditionally dormant (Baskin & Baskin 2014).

Many studies did not assess the proportion of embryoless seeds and embryo viability, which compromised the exact classification of seeds belonging to many investigated populations. However, choosing to disregard data from these populations could result in an underestimated number of dormant seeds, because high germinability allows straightforward ND classification whereas low germinability does not imply seed dormancy. Nongerminated seeds could be embryoless or unviable or dormant or a combination of these three variables (Baskin & Baskin 2014). Therefore, we established the following hierarchical criteria to assess the occurrence of dormancy in seeds which germinated less than 70% and lacked viability tests (criteria 3, 4 and 5 were considered as inferences):

- Comparison of germinability at day 30 to final germination after longer periods of incubation. This criterion applied for two populations.
- 2- Comparison of control seeds with seeds that received any given treatment (storage, incubation with giberellic acid, scarification, fast drying process and experimental pollination) that increased germination. This criterion applied for 27 populations.
- 3- Correction of germination percentages using a conservative extrapolated number of viable seeds. Briefly, information on embryoless and unviable seeds of *campos rupestres* was analyzed separately for each family. The lowest percentage of embryoless seeds was combined with the lowest percentage of unviable seeds. This value was subtracted from 100%,

resulting in a conservative extrapolated percentage of viable seeds per taxon. Reported germination percentages were then corrected based on the extrapolated values and these values were used to classify seeds. This approach was used for populations of Cactaceae, Poaceae, Velloziaceae and Verbenaceae. Calculation of Melastomataceae seeds was exceptionally performed according to the tribes Melastomeae, Miconieae and Microlicieae independently (Appendix S4, Supporting information).

- 4- Correction of germination percentages using the highest germination percentages as a reference number of viable seeds. No population of Eriocaulaceae included in this study presented viability tests to help inference. Only one population of Bromeliaceae had embryo presence and viability investigated, and it did not belong to the same genus as the three populations that needed reference value. Thus, we used the mean germinability of seeds that germinated more than 80% as a value of seed viability (Appendix S4, Supporting information).
- 5- Correction of germination percentage assuming the same viability of a congeneric species. In a single case, *Diplusodon hirsutus* germination percentage was calculated based on viability values of *Diplusodon orbicularis* (Appendix S4, Supporting information).

Classification outcome was considered non-conclusive when seeds did not germinate and there was no reference value for seed viability or when seed viability was less than 10%.

#### Occurrence of seed dormancy in campos rupestres seeds

Baskin and Baskin (2014) collected a massive amount of information on seed dormancy and germination worldwide, from all main vegetation zones. Comparison of campos rupestres data on seed dormancy with Baskin and Baskin (2014) database allows us to situate *campos rupestres* within their encompassing biome and other vegetation zones worldwide. Campos rupestres are part of the cerrado biome in Brazil, which is further classified as a tropical savanna (Oliveira-Filho & Ratter, 2002). Therefore, information on primary seed dormancy of populations growing in *campos* rupestres was compared to data of species growing in savannas (i.e. tropical dry woodlands, natural savannas and grasslands) and in all the major vegetation types worldwide according to Baskin and Baskin (2014). We used Chi-square to contrast frequencies of nondormancy (ND) and dormancy (D) in campos rupestres, savannas and worldwide. Savanna species with two reported dormancy states were separated in two populations and both states were considered. Yates correction for continuity was used in calculating Chi-square test whenever necessary (i.e. low expected values in the contingency table). Although populations of campos rupestres with dormant and nondormant (D+ND) seeds are shown, their data were not included in this analysis, since such category does not correspond to any of the broadly defined categories used by Baskin and Baskin (2014).

To understand the evolution of seed dormancy in *campos rupestres*, families were arrayed on a phylogenetic tree and qualitatively analyzed. Briefly, phylogeny for the represented families was obtained using 'Phylomatic'

(http://phylodiversity.net/phylomatic/). The resulting phylogeny was then imported into 'Mesquite' (http://mesquiteproject.org/) to generate the tree. We plotted D, D+ND and

ND percentages of each represented family in the tree and visually searched for patterns on dormancy occurrence.

#### **Ecological correlates of seed dormancy**

We were able to obtain missing information on species life form via Reflora database (http://reflora.jbrj.gov.br). Missing information on dispersal mode was inferred based on our knowledge on fruit morphology (Barroso *et al.* 1999). Finally, we retrieved other relevant information, such as seeds collection dates and experiment duration, not mentioned in studies in which we participated.

Date of seed collection or fruit dispersal phenology was used to determine the time of seed dispersal, which was further distributed in four seasons according to pluviometric data of Serra do Cipó (Madeira & Fernandes 1999). Early-rainy season comprises the months from October to December, while late-rainy season lasts from January to March. Early-dry season comprises the months from April to June, and late-dry season lasts from July to September.

Since our analysis aims primarily on restrictions imposed by length of water deficit (in months), we simplified microhabitat data considering populations of mesic, mesic/xeric or wet habitat as mesic. Species classified as belonging to xeric/mesic habitats were excluded from the microhabitat analysis.

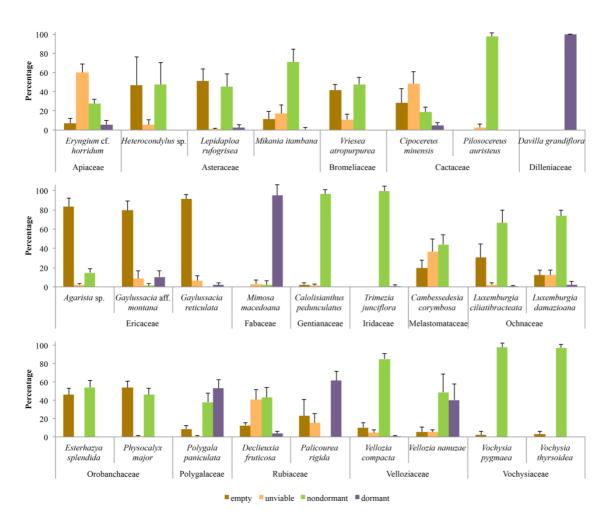
Chi-square tests were used to determine differences in the frequency of seed dispersal among seasons, and the occurrence of seed dormancy across seasons, microhabitat and dispersal mode (Zar 2012). In each life-form category and in each season of seed dispersal, chi-square tests were used to compare the number of observed populations to the number of expected populations in the same category under a constant D, D+ND and ND proportion.

#### RESULTS

#### Viability and germination experiments

Seeds of *Palicourea rigida*, *Davilla grandiflora*, *Mimosa macedoana*, *Gaylussacia reticulata*, *Gaylussacia* aff. *montana* and *Agarista* sp. showed low (<15%) or null germination. A high percentage of *P. rigida*, *D. grandiflora* and *M. macedoana* seeds remained viable after the germination trials and were considered dormant. The three Ericaceae species - *G.* aff *montana*, *G. reticulata* and *Agarista* sp. - had at least 80% of embryoless seeds, and most viable seeds of *G.* aff *montana* were also dormant.

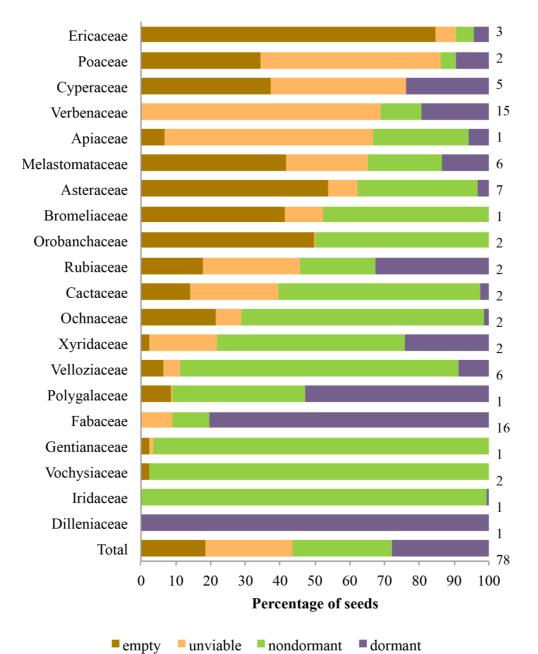
Trimezia junciflora, Vochysia pygmaea, Vochysia thyrsoidea, Pilosocereus auristeus, Calolisianthus pedunculatus, Vellozia compacta, Luxemburgia damazioana and Mikania itambana had high germination percentages (>70%) considering the total number of seeds. Germination of these species was greater than 97% when only viable seeds were considered. Germination of the 11 other species ranged from 80% to 100% of viable seeds. Polygala paniculata and Vellozia nanuzae had intermediate germination percentages, and also presented seeds that remained viable after the germination trials (Figure 1).



**Figure 1.** Mean percentages of empty, unviable, nondormant and dormant seeds of 26 *campos rupestres* species (original data). Total of viable seeds are the sum of nondormant and dormant seeds percentages. Error bars indicate standard deviation.

#### Seed viability in campos rupestres seeds

In this study, we were able to gather information from 231 populations of 27 families. However, embryo presence and viability were assessed in only 78 (34%) populations of 20 (74%) families. On average,  $56.3\% \pm 33.5$  (mean  $\pm$  SD) of *campos rupestres* seeds were considered viable,  $27.7\% \pm 32.4$  were dormant and  $28.6\% \pm 32.3$ were nondormant. The remaining seeds were either empty  $18.6\% \pm 26.5$  or unviable  $25.1\% \pm 28.6$ . Despite this high percentage of empty and unviable seeds, nine families



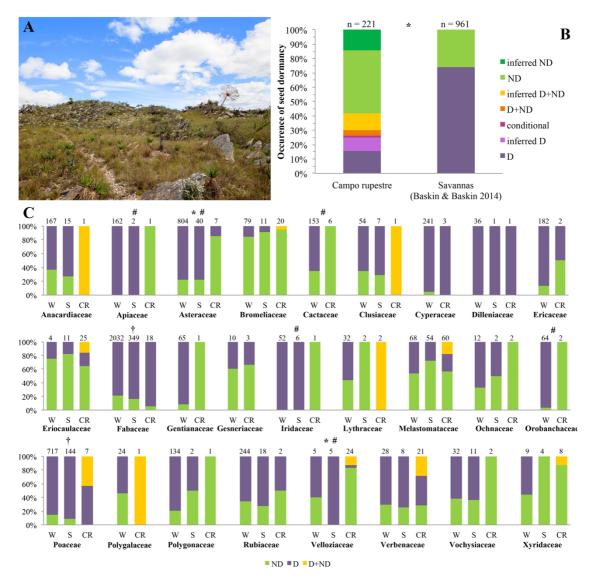
had more than 70% of viable seeds. Three families presented less than 24% of viable seeds and viable seeds of the other eight families ranged from 31 to 60% (Figure 2).

**Figure 2.** Mean percentages of empty, unviable, nondormant and dormant seeds from campos rupestes populations per family. Total of viable seeds are the sum of nondormant and dormant seeds percentages. Data labels next to bars indicate number of sampled populations (n). Only experiments that performed the tetrazolium test were included, except for Fabaceae for which data on scarified seeds were also considered as a viability assessment.

#### Seed dormancy in campos rupestres seeds

Plants with nondormant (ND) seeds predominated among 221 populations of *campos rupestres* (Figure 3B). In total, 97 populations (44%) had ND seeds, and other 32 (14%) had seeds with inferred ND, making a total of 58% of all populations with ND seeds. Among the 58 populations (26%) with dormant (D) seeds, 21 (9%) were inferred dormant and three had conditional dormancy. Dormant and nondormant (D+ND) seeds occurred in nine populations and were inferred in other 25 populations growing in *campos rupestres*, totalling 34 populations (15%). Ten species were designated as non-conclusive due to large number of unviable seeds or to the lack of reference value for seed viability, and one of them (*Pilostyles blanchetii*) was the sole representative of Apodanthaceae, resulting in a total of 26 plants sampled families.

Altogether, *campos rupestres* frequencies of ND and D were markedly different from frequencies reported for savannas (Baskin & Baskin 2014). ND was more frequent in *campos rupestres* compared to savannas ( $\chi^2$ = 129.89, p < 0.001; Figure 3B). However, ND and D frequencies of most families were not different between *campos rupestres* and savannas, and neither from worldwide frequencies. ND was more frequent in Asteraceae and Velloziaceae of *campos rupestres* compared to savannas ( $\chi^2$ =12.7, p<0.001;  $\chi^2$ =5.7, p=0.017; respectively) and to all vegetations worldwide combined ( $\chi^2$ =8.2, p=0.004;  $\chi^2$ =15.6, p<0.001; respectively). *Campos rupestres* and worldwide frequencies were also different for Apiaceae ( $\chi^2$ =40.2; p<0.001), Cactaceae ( $\chi^2$ =7.7; p=0.005), Iridaceae ( $\chi^2$ =8.2; p=0.004) and Orobanchaceae ( $\chi^2$ =17.2; p<0.001). Savanna and worldwide frequencies were only different for Fabaceae ( $\chi^2$ =4.2; p=0.04) and Poaceae ( $\chi^2$ =4.0; p=0.046; Figure 3C).



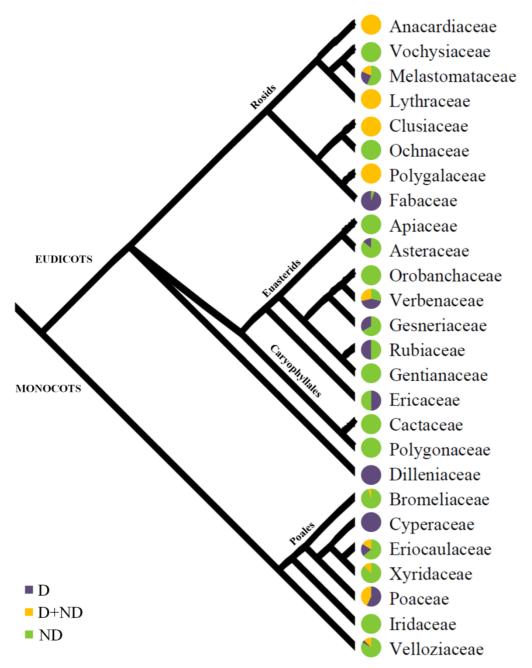
**Figure 3.** Comparison of seed dormancy occurrence across different scales. A) A photograph of *campos rupestres* landscape with typical mosaic of grasslands and rocky outcrops. B) Comparison of seed dormancy occurrence between savannas (according to Baskin & Baskin 2014) and *campos rupestres*. C) Comparison of seed dormancy occurrence in 26 plant families in all major vegetation types worldwide (W) and in savannas (S) according to Baskin and Baskin (2014) and *campos rupestres* (CR). Seeds were categorized as nondormant (ND), dormant and nondormant (D+ND) or D (dormant). Data label above bars indicate number of samples (n). Symbols indicate differences between D and ND frequencies worldwide and in *campos rupestres* (#), in *campos rupestres* and savannas (\*), worldwide and in savannas (†), according to Chi-squared tests.

Although D, D+ND and ND may have a phylogenetic signal (i.e. can be

concentrated in certain families; dormant seeds in the Fabaceae and non-dormant seeds

in the Velloziaceae), dormancy was evolutionarily labile. We found a random

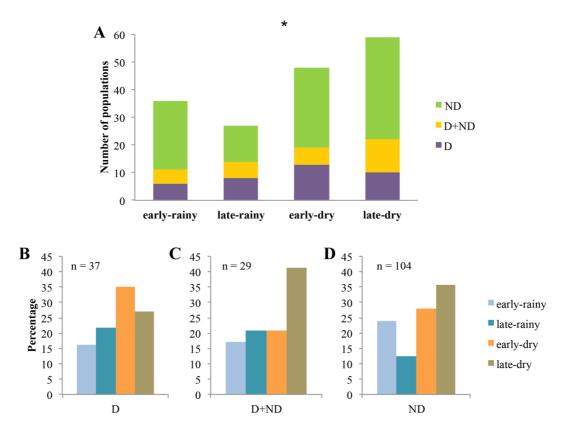
distribution of dormancy occurrence across seed plants from *campos rupestres* in major clades (i.e. D, D+ND and ND occur in Monocots, Rosids and Euasterids; Figure 4). This suggests that seed dormancy evolved multiple times in *campos rupestres*.

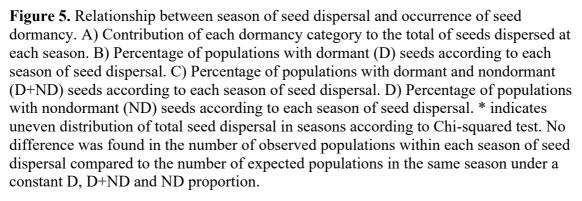


**Figure 4.** Relationship between phylogeny and occurrence of seed dormancy. A) Phylogeny of the seed plants (Spermatophyta) of campos rupestres. Pie charts at the tips of the tree represent the proportion of dormancy classes (by population) within each family. Most representative groups were labeled to highlight the distribution of families within Monocots and Eudicots clades. ND, nondormant; D+ND, dormant and nondormant; D, dormant.

#### **Ecological correlates of seed dormancy**

The distribution of seed dispersal across seasons was uneven for *campos rupestres* populations ( $\chi^2$ =13.8, p=0.003). Most populations 59 (35%) dispersed seeds during late-dry season, while only 27 (16%) dispersed during late-rainy season. Overall, 107 populations dispersed seeds during dry season, while 63 dispersed seeds during rainy season (Figure 5A). In addition, we found no evidence of seasonal patterns for seed dormancy occurrence. The distribution of seed dispersal in seasons was not different than expected for D (p= 0.48; Figure 5B), D+ND (p=0.66; Figure 5B) and ND (p=0.76; Figure 5C) seeds.





Our data comprises more populations from xeric than mesic micro-habitats, more abiotic than biotic dispersal and less trees than herbs and shrubs. We found no significant relationship between ecological variables - micro-habitat, life form and dispersal mode - and seed dormancy occurrence (<u>Table 1</u>).

Variables	total n	D		ND		•		10
		n	%	Ν	%	χ2	р	df
Micro-habitat	155							
xeric	127	43	33.9	84	66.1	2.748	0.10	1
mesic	28	5	17.9	23	82.1	2.748	0.10	1
Life form	179							
herb (obs)	71	20	28.2	51	71.8	0.50	0.45	1
herb (exp)	71	23	32.4	48	67.6	0.58	0.45	1
shrub (obs)	00	37	37.4	62	62.6	1 1 5	0.20	1
shrub (exp)	99	32	32.4	67	67.6	1.15	0.28	1
tree (obs)	0	1	11.1	8	88.9	2	0.1.5	
tree (exp)	9	3	32.4	6	67.6	2	0.15	1
Dispersal Mode	187							
abiotic	159	52	32.7	107	67.3	1 415	0.224	1
biotic	28	6	21.4	22	78.6	1.413	0.234	1

**Table 1.** Distribution of dormant (D) and nondormant (ND) seeds according to microhabitat, life form and dispersal mode.

Note: number of observed populations (obs) within each life form category was compared to the number of expected populations (exp) in the same category under a constant D and ND proportion in all life forms.

#### DISCUSSION

Our findings show that frequencies of nondormancy greatly differed *among campos rupestres* and their encompassing biome, i.e. savannas (Baskin & Baskin 2014). To the best of our knowledge, ND is more frequent in *campos rupestres* than in savannas or any other vegetation zone on Earth. Given that phylogenetic analyses point to dormancy as an ancestral state of seeds (Willis *et al.* 2014), our data suggest that dormancy was independently lost multiple times in many phylogenetic unrelated groups of *campos rupestres*, which indicates a convergent evolution. However, none of the ecological aspects analyzed here – season of seed dispersal, microhabitat, life form or dispersion mode – was able to shed a light on this matter. The distribution of seed dispersal across seasons was uneven for *campos rupestres* populations, indicating that evolution may have favored a control over timing of seed dispersal rather than a control over germination timing to increase chance of seedling survival. We also found an unprecedented wide variation in the amount of empty and unviable seeds within a single vegetation, which suggests a large variation on the potential of sexual reproduction between populations and families. Notably, *campos rupestres* have major particularities in regard to the known patterns of seed ecology. These differences could be part of singularities found in climatically stable, constant and infertile environments (Hopper 2009).

Seed dormancy is more frequent than non-dormancy (Baskin & Baskin 2004, 2014) across all vegetations, and its frequency is further incremented in environments with seasonal frost and/or drought (Jurado & Flores 2005, Baskin & Baskin 2014). Since *campos rupestres* belong to the savanna biome and both are under the influence of a 4–6-month dry season (Madeira & Fernandes 1999), we expected to find a proportion of ND populations similar to savannas. However, we found that 58% of tested populations of *campos rupestres* are ND, a more than 2-fold higher difference compared to that reported values from savannas (26%). ND is more important in *campos rupestres* than even in tropical rainforests (48.7%), where ND was considered to be more important than in any other vegetation zone (Baskin & Baskin 2014). As far as we are concerned, our community-level assessment of seed dormancy represents the only vegetation in the world where ND seeds predominate over D seeds.

Other studies have investigated dormancy at the community-level in specific vegetation types, and found proportions that did not depart from those reported for their vegetation zones with worldwide samples (Sautu *et al.* 2006, Wang *et al.* 2012, Liu *et al.* 2014). However, Gross and Vary (2014) found about 46% of ND among 134 species growing in sandy woodlands in Eastern Australia - a percentage only similar to tropical rainforests - and Wang *et al.* (2009) found a bimodal distribution of germination percentages of arid and semi-arid zone species from northwest China. At least three factors may explain these distinctive patterns of dormancy occurrence of a community regarding its vegetation zone: spatial heterogeneity that leads to different biotic and abiotic filters, the assembly and disturbance history of the community (Chase 2003), and the coexistence of different germination strategies under unfavorable environmental conditions (Greenberg *et al.* 2001).

All three factors may play a role in determining *campos rupestres* singularity. Spatial heterogeneity has been widely reported for savannas (Augustine 2003, Gillson 2004, Silva *et al.* 2006) and studies have already shown an association between germination traits of *campos rupestres* species and their ecological breadths (Ranieri *et al.* 2011, Marques *et al.* 2014). Evidences also suggest that the assembly and disturbance history of *campos rupestres* and *cerrado* communities are quite different from each other. Alves and Kolbek (1994) concluded that *campos rupestres* are edaphically isolated from the surrounding *cerrado*, and that most known endemic species of *campos rupestres* have probably originated locally from common ancestral species. Finally, important endemic families of *campos rupestres*, such as Eriocaulaceae and Xyridaceae, have small and spherical seeds with an absolute light requirement for germination (Abreu & Garcia 2005, Oliveira & Garcia 2011). This kind of seeds tend to be more easily buried in the soil, which increases the probability of their incorporation

into soil seed banks (Hölzel & Otte 2004) even in the absence of primary dormancy. Thus, light requirement may be a germination strategy that functions partly as a mechanism controlling seed bank dynamics and seedling emergence. Due to the abovementioned factors, emergence of new patterns for *campos rupestres* from fine-scale analysis should come as no great surprise. Further investigation on community level of other savanna physiognomies are needed improve our understanding of the ecology and evolution of seed dormancy within the biome.

In addition, the database we have compiled for *campos rupestres* in the literature may be biased toward certain groups, giving us a limited insight about seed dormancy occurrence, but this is often the case in studies of this nature. However, our data comprise many of the most dominant families of *campos rupestres*, such as Velloziaceae, Melastomataceae, Eriocaulaceae and Xyridaceae (Giulietti *et al.* 2005, Alves & Kolbek 2010). Thus, despite the limited size of the database, we are confident that, although small, it is representative of the vegetation.

Given the exceptionally unique high proportion of ND found in *campos rupestres*, we investigated in which phylogenetic level this singularity could stem from. We first tested for differences within families. Although we have not found statistical differences between ND and D frequencies for most families in *campos rupestres* compared to savannas or to all major vegetation types worldwide, many families had a very low representation (less than five populations) in our survey, making it difficult to draw accurate conclusions. However, non-significant trends (p<0.10) were observed towards higher frequencies of ND in *campos rupestres* than worldwide in seven families (Bromeliaceae, Gentianaceae, Melastomataceae, Ochnaceae, Polygonaceae, Vochysiaceae and Xyridaceae). The same trend towards ND was observed in Apiaceae and Vochysiaceae of *campos rupestres* compared to savanna. Thus, differences in ND

frequencies within families should be at least partially responsible for the higher overall frequency of ND in *campos rupestres*.

Willis et al. (2014) used a comprehensive dataset comprising over 14,000 taxa in 318 families and found morphophysiological dormancy to be the most likely ancestral state of seed plants and loss of dormancy to be a highly derived state, present primarily at the tips of the phylogeny. Along with Silveira et al. (2012), our data corroborates this finding, evidencing a large degree of homoplasy in dormancy/nondormancy occurrence across seed plants from *campos rupestres*, with an apparently convergent evolution toward ND. Rees (1993, 1994) modeled the effects of adult longevity, timing of reproduction and population age/stage structure on the evolution of seed dormancy in constant and variable environments. He found that the evolutionarily stable strategy in constant environments is for ND seeds regardless of the other factors. In a variable environment, increased adult longevity generally selected against seed dormancy (Rees 1993). Our results, therefore, agree with this model, since *campos rupestres* are geologically and geomorphologically old and stable environments (Saadi 1995), edaphically isolated from surrounding vegetation changes over past climatic shifts (Alves & Kolbek 1994) and have high prevalence of long-lived stress-tolerance species (Negreiros et al. 2014).

Since dormancy enables seeds to avoid germination during periods that are only ephemerally favorable (Baskin & Baskin 2014), we expected seed dormancy to be associated with dispersion in an unfavorable time for seedling establishment, that is late-rainy season, just before a five month drought (Silveira *et al.* 2012). Contrary to our prediction, seed dormancy was not associated with seed dispersal seasons. However, the distribution of total seed dispersal across seasons was uneven for *campos rupestres*, and late-rainy season had the lowest number of populations dispersing seeds. Therefore,

control over timing of seed dispersal seems to play a more important role than seed dormancy in synchronizing seedling establishment with optimum conditions. Additionally, studies have indicated that seeds of populations growing in *campos rupestres* that do not germinate at early-rainy season (such as positive photoblastic, buried seeds) can develop secondary dormancy and remain in that state until the end of the subsequent dry season (Garcia *et al.* 2012, Garcia *et al.* 2014). Finally, there is little evidence that *campos rupestres* species evolved competition-related traits (Negreiros *et al.* 2014), and therefore, we should not expect dormancy to have evolved as a response to competition with the parent plant (Rees 1996). Thus, germination timing and secondary dormancy are likely to play a more important role in avoiding germination under unfavorable conditions for seedling establishment in *campos rupestres* than primary dormancy.

A multitude of reports have shown the relationship between microhabitat (e.g. light intensity, soil moisture, soil salinity) and seed germination (Baskin & Baskin 2014). Although all populations in a given habitat are exposed to similar conditions, different microhabitats created by environmental heterogeneity – of soils and topography, for instance (Alves & Kolbek 2010) – can exert different kinds of selective pressure on seedling establishment. In *campos rupestres*, xeric habitats present very low levels of soil moisture during dry season (Coelho *et al.* 2006) correlated with extremely high seedling mortality (Coelho *et al.* 2008), which is probably attenuated in mesic sites. In fact, Silveira *et al.* (2012) reported a significant association of dormant species and xeric microhabitats in Melastomataceae of *campos rupestres*. However, our community analysis did not support this finding, since proportions of dormant populations in our database did not differ among mesic and xeric sites. Therefore, the

relationship between seed dormancy and microhabitat might be phylogenetically dependent or restricted.

We also did not find evidence of association between seed dormancy and life form or dispersal mode for populations growing in *campos rupestres*. Effects of these ecological correlates on seed germination seems to vary over different communities (Sautu *et al.* 2007, Wang *et al.* 2012, Gross & Vary 2014, Liu *et al.* 2014, Xu *et al.* 2014), and patterns that have emerged from global analysis do not meet the existing theoretical models, probably due to other more influent factors that select for dormancy (Jurado & Flores 2005). Seed dormancy (or its absence) is part of the plant life cycle, which in turn is influenced by a complex interaction between environmental and genetic factors in each life stage (Burghardt *et al.* 2015). Disentangling the contributions of multiple factors that influence the occurrence of seed dormancy is vital to make further progress. Unfortunately, gathering a wide range of information on a representative number of species is quite a challenging task, since studies have diverse focuses and standardizations.

Our study shows that populations from *campos rupestres* presented a great diversity of seed germination patterns, with interspecific and interfamilies differences. All ten species, belonging to Poaceae, Cyperaceae and Ericaceae families had only sporadic germination and produced high percentages of empty or unviable seeds, therefore presenting a very low investment in sexual reproduction. This result can be related to the phosphorus (P)-impoverished soils of *campos rupestres*, one of the most P-deficient soils in the world (Oliveira *et al.* 2015). P limitation is correlated with low investment in sexual reproduction which restricts P losses (Fujita *et al.* 2014), since reproductive organs are naturally P-rich (Kerkhoff *et al.* 2006) and seeds of species naturally occurring in severely P-impoverished landscapes are even P-richer (Lambers *et al.* 2010). Other possible explanations to the low number of viable seeds in those three families reside on: breeding system limitation, such as pollen limitation; genetic load, which occurs in populations that become reliant on clonal reproduction as a means of reproductive assurance; and/or investment in a resprouting strategy, which provides persistence in the environment as an alternative to establishment from seeds after fires (Hoffmann 1998, Lamont & Wiens 2003, Montoro & Santos 2007, Holmes *et al.* 2008, Fidelis *et al.* 2010, Vos *et al.* 2012). These four factors, however, do not seem to apply to Fabaceae, Velloziaceae and Vochysiaceae populations, which present high levels viability, and seemed to affect to a lesser extent the Ochnaceae, Orobanchaceae, Rubiaceae and Xyridaceae populations, whose seeds presented intermediary percentages of viability. Populations of Asteraceae, Cactaceae, Melastomataceae and Verbenaceae presented a wide range of seed viability percentages, indicating interespecific variation or environmental influence (Feitosa *et al.* 2009, Silveira *et al.* 2012).

Our data have also important implications for the restoration of *campos rupestres*. To this date, many techniques were inefficient to restore plant community of *campos rupestres* (Matias *et al.* 2009, Le Stradic *et al.* 2014a,b). We found an overall mean of 44% of empty and unviable seeds, which indicates that the amount of seeds necessary for the effective use of wild species seeds in restoration can be unfeasibly large. Achieving effective landscape-scale restoration will need seed banks to go beyond the core skills of collection and storage of germplasm and scale-up capacity in seed production and technology to improve wild seed use in restoration (Merritt & Dixon 2011). Additionally, given that phylogeny seems to play an important role in determining seed viability percentages in many families, our study provides an useful

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overview for species selection and devising of new approaches for seed-based restoration techniques.

It is also important to highlight that most studies of *campos rupestres* seeds fail to document or understand the viability of collected seeds at time of seed dispersal, resulting in no knowledge of the potential of the seed resource to produce plants. Therefore, it is important to standardize seed viability/dormancy research and improve communication of results in order to make studies comparable and hence allow a useful understanding of seed ecology of *campos rupestres* seeds and comparable vegetations (Hilhorst 2011, Silveira 2013, Baskin & Baskin 2014).

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#### APPENDIX

## **Appendix S1**

Keywords used for topic search in Web of Science (http://thomsonreuters.com/web-of-knowledge/):

- (campo\* rupestre\* OR rupestrian grassland\* OR rocky outcrop\* OR rupestrian field\* OR canga\* OR rocky field\*) AND germination AND seed\*
- grassland AND germination AND seed AND Brazil

Keywords used for all indexes search in Scielo (http://scielo.br/):

- (campo rupestre OR *campos rupestres* OR rupestrian grassland OR rupestrian grasslands OR rocky outcrop OR rocky outcrops OR rupestrian field OR rupestrian fields OR rupicolous field OR rupicolous fields OR rupicolous grassland OR rupicolous grasslands OR canga OR rocky field OR rocky fields)
   AND seed AND germination
- (campo rupestre OR *campos rupestres* OR canga) AND (semente OR sementes)
   AND germinação

Keywords used for search "anywhere in the article" in Google Scholar (http://scholar.google.com.br/):

seed germination Brazil "campo rupestre" OR "campos rupestres" OR
 "rupestrian grassland" OR "rupestrian field" OR "rocky outcrop"

## Appendix S2

Dormancy (D), dormancy and non-dormancy (D+ND) or nondormancy (ND) in seeds of *campos rupestres*. \*=occurence of dormancy is inferred from available information on germination, treatments and on characteristics of seeds in that family, tribe or genus. Microhabitat: x/m, xeric/mesic; m/w, mesic/wet; x/m/w, xeric/mesic/wet. Dispersal period: ER, early-rainy; LR, late-rainy; ED, early-dry; LD, late-dry.

Family/ species (population)	Dormancy class	Viability assessment	Life form	Dispersal Mode	Micro- habitat	Dispersal period	Reference
Anacardiaceae							
Tapirira obtusa	D+ND	treatment	tree	biotic	mesic	LR	36
Apiaceae							
Eryngium cf. horridum	ND	tetrazolium test	herb	abiotic	xeric	LR	1
Apodanthaceae							
Pilostyles blanchetii	nc	none	parasite	biotic	xeric	-	3
Asteraceae							
Baccharis retusa	ND	none	shrub	abiotic	-	LD	8
Eremanthus incanus	ND	tetrazolium test	tree	abiotic	xeric	ER	57
Heterocondylus sp.	ND	tetrazolium test	shrub	abiotic	xeric	LD	1
Lepidaploa rufogrisea	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Lessingianthus linearifolius	ND	tetrazolium test	shrub	abiotic	xeric	-	16
Lychnophora pinaster	D	treatment	shrub	abiotic	xeric	ER	21, 20, 22
Mikania itambana	ND	tetrazolium test	shrub	abiotic	xeric	LD	1
Richterago arenaria	nc	tetrazolium test	herb	abiotic	xeric	LR	16
Bromeliaceae							
Aechmea nudicaulis	ND	none	herb	biotic	x/m	LR	19
Alcantarea imperialis	ND	none	herb	abiotic	xeric	ER	35

Cryptanthus schwackeanus	ND	none	herb	biotic	xeric	ED	19
Dyckia saxatilis*	ND	extrapolated	herb	abiotic	xeric	LR	19
Dyckia sordida*	D+ND	extrapolated	herb	abiotic	xeric	ED	56
Dyckia ursina	ND	none	herb	abiotic	xeric	ED	56
Encholirium heloisae	ND	none	herb	abiotic	xeric	ED	56
Encholirium magalhaesii	ND	none	herb	abiotic	xeric	ED	56
Encholirium pedicellatum	ND	none	herb	abiotic	xeric	ED	56
Encholirium reflexum	ND	none	herb	abiotic	xeric	ED	56
Encholirium scrutor*	ND	extrapolated	herb	abiotic	xeric	ED	56
Encholirium subsecundum	ND	none	herb	abiotic	xeric	ED	56
Neoregelia bahiana	ND	none	herb	biotic	xeric	ED	19
Pitcairnia flammea	ND	none	herb	abiotic	xeric	LD	35
Tillandsia stricta	ND	none	herb	abiotic	x/m	ED	19
Vriesea atropurpurea	ND	tetrazolium test	herb	abiotic	xeric	ED	1
Vriesea bituminosa	ND	none	herb	abiotic	x/m	LR	19
Vriesea crassa	ND	none	herb	abiotic	xeric	ED	19
Vriesea friburgensis	ND	none	herb	abiotic	mesic	LD	19
Vriesea minarum	ND	none	herb	abiotic	xeric	ED	19
Cactaceae							
Arthrocereus glaziovii*	ND	extrapolated	succulent	biotic	xeric	LR	5
Arthrocereus melanurus subsp. Magnus	ND	none	succulent	biotic	xeric	LR	5
Arthrocereus melanurus subsp. Melanurus	ND	none	succulent	biotic	xeric	LR	5
Arthrocereus melanurus subsp. Odorus	ND	none	succulent	biotic	xeric	LR	5
Cipocereus minensis	ND	tetrazolium test	succulent	biotic	xeric	LD	1
Pilosocereus aurisetus	ND	tetrazolium test	succulent	biotic	xeric	ED	1
Clusiaceae							
Kielmeyera regalis*	D+ND	treatment	shrub	abiotic	xeric	LD	39
Cyperaceae							
Lagenocarpus albo-niger	nc	tetrazolium test	herb	abiotic	xeric	ER	16
Lagenocarpus tenuifolius	D	tetrazolium test	herb	abiotic	xeric	-	16

Rhynchospora ciliolata	nc	tetrazolium test	herb	abiotic	xeric	LR	16
Rhynchospora consanguinea	D	tetrazolium test	herb	abiotic	xeric	ER	16
Rhynchospora riedeliana	D	tetrazolium test	herb	abiotic	xeric	LR	16
Dilleniaceae							
Davilla elliptica	D	tetrazolium test	shrub	biotic	xeric	LR	1
Ericaceae							
Agarista sp.	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Gaylussacia aff. montana	D	tetrazolium test	shrub	biotic	xeric	ED	1
Gaylussacia reticulata	nc	tetrazolium test	shrub	biotic	xeric	ED	1
Eriocaulaceae							
Actinocephalus geniculatus	ND	none	herb	abiotic	xeric	-	15
Actinocephalus incanus	ND	none	herb	abiotic	xeric	-	15
Comanthera aciphylla	ND	none	herb	abiotic	xeric	LD	30
Comanthera bisulcata (Serra do Cipó)*	D	none	herb	abiotic	mesic	LD	12, 30
Comanthera bisulcata (Diamantina)*	D	extrapolated	herb	abiotic	mesic	-	31
Comanthera brasiliana	ND	none	herb	abiotic	xeric	ER	28
							12, 26, 31,
Comanthera elegans (Diamantina)	ND	none	herb	abiotic	x/m	LD	34, 27
Comanthera elegans (Serra do Cipó)	ND	none	herb	abiotic	x/m	LR	46, 32
Comanthera elegantula (Diamantina)	ND	none	herb	abiotic	x/m	LD	31
Comanthera elegantula (P. E. Rio Preto)*	D+ND	extrapolated	herb	abiotic	x/m	LD	34
Comanthera magnifica (brancona morphotype)*	D	extrapolated	herb	abiotic	xeric	ER	28
Comanthera magnifica (branquinha							
morphotype)*	D	extrapolated	herb	abiotic	xeric	ER	28
Comanthera mucugensis*	D+ND	extrapolated	herb	abiotic	x/m	-	33
Comanthera nivea*	ND	extrapolated	herb	abiotic	x/m	ED	46
Comanthera suberosa	ND	none	herb	abiotic	xeric	LD	28
Paepalanthus chiquitensis*	ND	extrapolated	herb	abiotic	x/m	-	42
Paepalanthus chlorocephalus	ND	none	herb	abiotic	mesic	-	15
Paepalanthus senaeanus	ND	none	herb	abiotic	mesic	-	15

Syngonanthus anthemiflorus	ND	none	herb	abiotic	xeric	LD	12, 30
Syngonanthus caulescens*	D	extrapolated	herb	abiotic	wet	LD	30
Syngonanthus gracilis	ND	none	herb	abiotic	xeric	LD	30
Syngonanthus nitens (large morphotype)*	D+ND	extrapolated	herb	abiotic	m/w	ER	29
Syngonanthus nitens (small morphotype)*	ND	extrapolated	herb	abiotic	m/w	ER	29
Syngonanthus vernonioides*	D+ND	extrapolated	herb	abiotic	xeric	ER	30
Syngonanthus verticillatus	ND	none	herb	abiotic	mesic	LD	12, 30
Fabaceae							
Calliandra fasciculata	ND	none	shrub	abiotic	mesic	ED	50
Chamaecrista cathartica	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista cipoana	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista dentata (P. E. do Itacolomi)	D	treatment	shrub	abiotic	-	ED	18
Chamaecrista dentata (Serra do Cipó)	D	treatment	tree	abiotic	xeric	-	13
Chamaecrista desvauxii var. latistipula	D	treatment	herb	abiotic	mesic	-	13
Chamaecrista desvauxii var. malacophylla	D	treatment	herb	abiotic	mesic	-	13
Chamaecrista desvauxii var. molissima	D	treatment	herb	abiotic	x/m	-	13
Chamaecrista latifolia	D	treatment	herb	abiotic	-	-	13
Chamaecrista mucronata	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista ochnacea var. purpurascens	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista ramosa	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista rotundifolia	D	treatment	herb	abiotic	xeric	-	13
Chamaecrista semaphora	D	treatment	shrub	abiotic	xeric	-	13
Chamaecrista venulosa	D	treatment	herb	abiotic	-	-	13
Mimosa calodendron	D	treatment	shrub	abiotic	xeric	ED	6
Mimosa foliolosa var. pachycarpa	D	treatment	shrub	abiotic	xeric	ED	51, 53
Mimosa macedoana	D	treatment	shrub	abiotic	xeric	LR	1
Gentianaceae							
Calolisianthus pedunculatus	ND	tetrazolium test	herb	abiotic	xeric	ED	1
Gesneriaceae							
Paliavana sericiflora	ND	none	shrub	abiotic	x/m	LD	40

Sinningia allagophylla	ND	none	herb	abiotic	x/m	LR	40
Sinningia rupicola	D	treatment	herb	abiotic	x/m	LR	40
Iridaceae							
Trimezia junciflora	ND	tetrazolium test	herb	abiotic	xeric	LD	1
Lythraceae							
Diplusodon hirsutus*	D+ND	extrapolated	shrub	abiotic	xeric	LD	55, 14
Diplusodon orbicularis*	D+ND	treatment	shrub	abiotic	xeric	ED	55, 14
Melastomataceae							
Acisanthera alsinaefolia*	ND	extrapolated	shrub	abiotic	mesic	LD	49
Acisanthera uniflora*	D	extrapolated	shrub	abiotic	xeric	ED	49
Cambessedesia corymbosa	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Cambessedesia hilariana	ND	none	shrub	abiotic	xeric	LD	49
Cambessedesia regnelliana	ND	none	shrub	abiotic	xeric	-	43
Chaetostoma armatum	D	tetrazolium test	shrub	abiotic	xeric	ED	49
Clidemia capitellata*	D	extrapolated	shrub	biotic	xeric	ER	49
Clidemia urceolata*	D+ND	extrapolated	shrub	biotic	xeric	ER	49
Comolia sertularia (Serra do Cabral)*	D	extrapolated	shrub	abiotic	xeric	ED	49
Comolia sertularia (Serra do Cipó)	D	tetrazolium test	shrub	abiotic	xeric	ED	49
Comolia sessilis*	D	extrapolated	shrub	abiotic	xeric	LD	49
Lavoisiera campos-portoana*	ND	extrapolated	shrub	abiotic	xeric	LD	49
Lavoisiera caryophyllea*	D	extrapolated	shrub	abiotic	mesic	ED	49
Lavoisiera confertiflora*	ND	extrapolated	shrub	abiotic	xeric	LD	49
Lavoisiera cordata*	D+ND	extrapolated	shrub	abiotic	xeric	LD	49, 38
Lavoisiera imbricata*	ND	extrapolated	shrub	abiotic	mesic	ER	49, 38
Lavoisiera pulcherrima*	D+ND	extrapolated	shrub	abiotic	mesic	LD	49
Lavoisiera subulata*	D+ND	extrapolated	shrub	abiotic	mesic	LD	49
Leandra aurea*	ND	extrapolated	shrub	biotic	xeric	ER	49
Leandra coriacea*	ND	extrapolated	shrub	biotic	xeric	ER	49
Lithobium cordatum*	D	extrapolated	herb	abiotic	xeric	ED	49
Macairea radula*	ND	extrapolated	shrub	abiotic	mesic	ER	49

Marcetia taxifolia*	ND	extrapolated	shrub	abiotic	xeric	LD	52, 49
Merianthera sipolisii*	D+ND	extrapolated	tree	abiotic	xeric	LR	49
Miconia albicans*	ND	extrapolated	shrub	biotic	xeric	ER	49
Miconia alborufescens*	ND	extrapolated	shrub	biotic	xeric	ER	49
Miconia angelana	ND	none	shrub	biotic	mesic	-	44
Miconia chamissois	ND	none	shrub	biotic	mesic	LD	49
Miconia cipoensis	ND	none	shrub	biotic	xeric	ER	49
Miconia corallina (P. E. do Itacolomi)*	ND	extrapolated	shrub	biotic	xeric	LR	49
Miconia corallina (Serra do Cipó)	D	tetrazolium test	shrub	biotic	xeric	ED	49
Miconia elegans	ND	none	tree	biotic	mesic	ER	49
Miconia ferruginata*	D+ND	extrapolated	tree	biotic	xeric	ER	49, 17
Miconia ibaguensis*	ND	extrapolated	shrub	biotic	mesic	LR	49
Miconia irwinii	ND	none	tree	biotic	xeric	LD	49, 17
Miconia ligustroides (Serra do Cipó)*	D+ND	extrapolated	shrub	biotic	xeric	ED	49
Miconia ligustroides (Serra do Gandarela)*	D	extrapolated	shrub	biotic	xeric	ED	54
Miconia pepericarpa*	D+ND	extrapolated	shrub	biotic	xeric	ED	54
Miconia rubiginosa*	ND	extrapolated	tree	biotic	xeric	ER	49
Miconia stenostachya*	D+ND	extrapolated	shrub	biotic	xeric	LR	49
Microlicia avicularis*	D	extrapolated	shrub	abiotic	xeric	LD	49
Microlicia graveolens*	ND	extrapolated	shrub	abiotic	mesic	LD	49
Microlicia inquinans*	ND	extrapolated	shrub	abiotic	xeric	-	43
Microlicia serpyllifolia*	ND	extrapolated	shrub	abiotic	xeric	LD	49
Microlicia tetrasticha*	D	extrapolated	shrub	abiotic	xeric	ED	49
Pterolepis alpestris*	D	extrapolated	shrub	abiotic	mesic	LD	49
Rhynchanthera cordata*	ND	extrapolated	shrub	abiotic	mesic	ER	49
Rhynchanthera grandiflora*	ND	extrapolated	shrub	abiotic	mesic	ER	49
Svitramia hatschbachii*	ND	extrapolated	shrub	abiotic	xeric	-	43
Svitramia minor*	ND	extrapolated	shrub	abiotic	xeric	-	43
Tibouchina candolleana	ND	none	tree	abiotic	mesic	ER	49
Tibouchina cardinalis	D+ND	tetrazolium test	shrub	abiotic	xeric	ED	49

Tibouchina heteromalla (Barão de Cocais)*	ND	extrapolated	shrub	abiotic	xeric	-	8
Tibouchina heteromalla (Lavras Novas)*	ND	extrapolated	shrub	abiotic	-	-	4
Tibouchina heteromalla (Serra do Cipó)*	D+ND	extrapolated	shrub	abiotic	xeric	LD	49
Tibouchina martiusiana*	D	extrapolated	shrub	abiotic	xeric	LD	49
Tibouchina papyrus	ND	treatment	tree	abiotic	xeric	-	23
Trembleya laniflora	ND	none	shrub	abiotic	xeric	LD	49, 41
Trembleya parviflora*	ND	extrapolated	shrub	abiotic	mesic	ER	49
Ochnaceae							
Luxemburgia ciliatibracteata	ND	tetrazolium test	shrub	abiotic	xeric	LD	1
Luxemburgia damazioana	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Orobanchaceae							
Esterhazya splendida	ND	tetrazolium test	parasite	abiotic	xeric	ER	1
Physocalyx major	ND	tetrazolium test	parasite	abiotic	xeric	LD	1
Poaceae			_				
Andropogon bicornis*	D+ND	extrapolated	herb	abiotic	x/m/w	LR	7
Andropogon leucostachyus*	D+ND	extrapolated	herb	abiotic	xeric	LR	7
Apochloa euprepes*	D	extrapolated	herb	abiotic	xeric	LR	7
Aristida torta	D	tetrazolium test	herb	abiotic	xeric	-	16
Cenchrus brownii*	D+ND	extrapolated	herb	abiotic	xeric	LD	7
Echinolaena inflexa (P. E. do Itacolomi)*	D	extrapolated	herb	abiotic	xeric	LR	7
Echinolaena inflexa (Serra do Cipó)	nc	tetrazolium test	herb	abiotic	xeric	LR	16
Setaria parviflora*	D	extrapolated	herb	abiotic	x/m	LR	7
Polygalaceae		-					
Polygala paniculata	D+ND	tetrazolium test	herb	abiotic	xeric	ED	1
Polygonaceae							
Coccoloba cereifera	ND	none	shrub	biotic	xeric	-	48
Rubiaceae							
Declieuxia fruticosa	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Palicourea rigida	D	tetrazolium test	shrub	biotic	xeric	LR	1
Velloziaceae							

Velloziaceae

V	Vellozia alata*	D+ND	extrapolated	shrub	abiotic	xeric	LR	25
V	Vellozia aloifolia	ND	none	shrub	abiotic	xeric	ER	24
V	Vellozia caruncularis	ND	tetrazolium test	herb	abiotic	xeric	ER	16
V	Vellozia ciliata	ND	none	herb	abiotic	xeric	ER	24
V	Vellozia compacta	ND	tetrazolium test	shrub	abiotic	xeric	ED	1
Į	Vellozia epidendroides	ND	tetrazolium test	shrub	abiotic	x/m	-	11, 16
Į	Vellozia gigantea	ND	none	tree	abiotic	xeric	-	9
V	Vellozia glabra	ND	none	shrub	abiotic	xeric	-	47
V	Vellozia glandulifera	ND	none	herb	abiotic	xeric	-	9
V	Vellozia glauca	ND	none	shrub	abiotic	xeric	ER	24
V	Vellozia hatschbachii	ND	none	shrub	abiotic	xeric	ER	24
V	Vellozia hirsuta	ND	none	shrub	abiotic	xeric	LD	24
V	Vellozia leptopetala	ND	none	shrub	abiotic	xeric	-	11
V	Vellozia maxillarioides*	D	extrapolated	shrub	abiotic	xeric	LD	24
V	Vellozia minima	ND	none	herb	abiotic	x/m	ED	24
V	Vellozia nanuzae	D+ND	tetrazolium test	shrub	abiotic	xeric	LD	1
V	Vellozia ornata*	D+ND	extrapolated	herb	abiotic	-	LD	24
V	Vellozia pusilla	ND	none	herb	abiotic	xeric	ED	24
V	Vellozia resinosa (P.E. Rio Preto)	ND	none	shrub	abiotic	-	LD	24
V	Vellozia resinosa (Serra do Cipó)	ND	tetrazolium test	shrub	abiotic	xeric	ER	16
V	Vellozia seubertiana	ND	none	shrub	abiotic	-	LD	24
V	Vellozia spiralis	ND	none	shrub	abiotic	-	LD	24
V	Vellozia stenocarpa	ND	none	shrub	abiotic	-	LD	24
V	Vellozia variabilis	ND	tetrazolium test	shrub	abiotic	xeric	-	9, 16
Ver	rbenaceae							
I	Lippia corymbosa*	ND	treatment	shrub	abiotic	xeric	-	37
I	Lippia diamantinensis (1)	D	treatment	shrub	abiotic	-	-	37
L	Lippia diamantinensis (2)*	ND	treatment	shrub	abiotic	-	-	37
I	Lippia filifolia	D	treatment	shrub	abiotic	-	-	37
L	Lippia florida*	D+ND	treatment	shrub	abiotic	xeric	-	37

Lippia hermannioides*	D	treatment	shrub	abiotic	xeric	_	37
Lippia lupulina*	nc	treatment	shrub	abiotic	xeric	-	37
Lippia origanoides (1)*	ND	treatment	shrub	abiotic	-	-	37
Lippia origanoides (2)	ND	treatment	shrub	abiotic	xeric	-	37
Lippia rotundifolia*	D+ND	treatment	shrub	abiotic	xeric	-	37
Stachytarpheta ajugifolia	D	tetrazolium test	shrub	abiotic	xeric	-	45
<i>Stachytarpheta commutata</i> (P.E. do Itacolomy)	D	tetrazolium test	shrub	abiotic	xeric	ER	45
Stachytarpheta commutata (P.E. do Rio Preto)	D	tetrazolium test	shrub	abiotic	xeric	-	45
Stachytarpheta confertifolia	D+ND	tetrazolium test	herb	abiotic	xeric	-	45
Stachytarpheta discolor	D+ND	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta glabra (Distrito de Curimataí)	nc	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta glabra (Morro do Chapéu)	nc	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta glabra (P.E. Rio Preto/ Heliporto)	D	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta glabra (P.E. Rio Preto/ Pico)	D	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta glabra (Serra do Rola Moça)	D+ND	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta harleyi	nc	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta martiana	D	tetrazolium test	shrub	abiotic	xeric	LD	45
Stachytarpheta sellowiana	ND	tetrazolium test	shrub	abiotic	xeric	LR	45
Stachytarpheta spathulata subsp. spathulata	D+ND	tetrazolium test	shrub	abiotic	xeric	-	45
Stachytarpheta sphatulata subsp. mogolensis	ND	tetrazolium test	shrub	abiotic	xeric	LD	45
Vochysiaceae							
Vochysia pygmaea	ND	tetrazolium test	shrub	abiotic	xeric	LD	1
Vochysia thyrsoidea	ND	tetrazolium test	tree	abiotic	xeric	LD	1
Xyridaceae							
Xyris bialata	ND	none	herb	abiotic	x/m	ED	10
Xyris cipoensis	ND	none	herb	abiotic	m/w	ED	2
Xyris longiscapa	ND	none	herb	abiotic	mesic	ED	2
Xyris obtusiuscula	D+ND	tetrazolium test	herb	abiotic	x/m	ER	16
Xyris peregrina			1 <b>1</b> .	abiotic	x/m	ED	10
	ND	none	herb	abiotic	X/111	ED	10

Xyris platystachia	ND	none	herb	abiotic	mesic	LD	2
Xyris trachyphylla	ND	none	herb	abiotic	mesic	LD	2

obs: Different populations of *Lippia diamantinensis* and *L. origanoides were identified as distinct species in the reference study, but were synonymized afterwards. We considered each of them different populations, distinguishing them with numbers.* 

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# Appendix S3

Family/ Species	Author	Collection date	Locality	Coordinate S	Coordinate W	Alt	number of individuals	replicates	seeds/ replicate
Apiaceae									•
Eryngium cf. horridum	Malme	15/03/2014	Serra do Cipó	19°14'	43°31'	1304	10	6	50
Asteraceae									
Lepidaploa rufogrisea	(A.StHil.) H.Rob.	19/04/2014	Lapinha da Serra	19°07'	43°40'	1175	10	6	40
Heterocondylus sp.		28/08/2013	Serra do Cipó	19°17'	43°35'	1215	12	6	25
Mikania itambana	Gardner	15/08/2013	Serra do Cipó	19°17'	43°35'	1215	30	6	25
Bromeliaceae									
Vriesea atropurpurea	Silveira	01/04/2014	Serra do Cipó	19°14'	43°31'	1304	40	6	50
Cactaceae									
Cipocereus minensis	(Werderm.) Ritter	15/08/2013	Serra do Cipó				1	6	50
Pilosocereus aurisetus	(Werderm.) Byles & G.D.Rowley	04/04/2014	Serra do Cipó	19°17'	43°35'	1263	1	6	50
Dilleniaceae	2								
Davilla grandiflora	A.StHil.	15/03/2014	Serra do Cipó	19°17'	43°35'	1215	22	6	15
Ericaceae									
Agarista sp.		04/04/2014	Serra do Cipó	19°14'	43°31'	1304	10	6	25
Gaylussacia aff. montana		19/04/2014	Lapinha da Serra	19°07'	43°40'	1175	10	6	25
Gaylussacia reticulata	Mart. ex Meisn.	19/04/2014	Lapinha da Serra	19°07'	43°40'	1175	10	6	25
Fabaceae									
Mimosa macedoana	Burkart	14/03/2014	Serra do Cipó	19°17'	43°35'	1142	10	4	25
Gentianaceae									
Calolisianthus pedunculatus	(Cham. & Schltdl.) Gilg	29/05/2014	Serra do Cipó	19°17'	43°35'	1215	4	6	50
Iridaceae	C								
Trimezia junciflora	(Klatt) Benth. & Hook.	15/08/2013	Serra do Cipó	19°17'	43°35'	1215	19	6	25

Melastomataceae									
Cambessedesia corymbosa	Mart. & Schrank ex DC.	04/04/2014	Serra do Cipó	19°17'	43°35'	1215	16	6	50
Ochnaceae									
Luxemburgia ciliatibracteata	Sastre	28/08/2013	Serra do Cipó	19°13'	43°29'	1309	7	6	50
Luxemburgia damazioana	Beauverd	04/04/2014	Serra do Cipó	19°17'	43°35'	1215	14	6	25
Orobanchaceae									
Esterhazya splendida	J.C.Mikan	12/10/2013	Serra do Cipó	19°17'	43°35'	1215	5	6	50
Physocalyx major	Mart.	19/09/2013	Serra do Cipó	19°17'	43°35'	1263	4	6	50
Polygalaceae									
Polygala paniculata	L.	08/05/2014	Serra do Cipó	19°17'	43°35'	1211	10	6	50
Rubiaceae									
Declieuxia fruticosa	(Willd. ex Roem. & Schult.) Kuntze	04/04/2014 to 11/06/2014	Serra do Cipó	19°17'	43°35'	1215	6	4	20
Palicourea rígida	Kunth	15/03/2014	Serra do Cipó	19°17'	43°35'	1215	10	6	50
Velloziaceae									
Vellozia compacta	Mart. ex Schult. & Schult.f.	05/04/2014	Lapinha da Serra	19°09'	43°39'	1137	10	6	50
Vellozia nanuzae	L.B.Sm. & Ayensu	04/04/2014 e 24/07/2014	Serra do Cipó	19°17'	43°35'	1263	10	6	35
Vochysiaceae									
Vochysia pygmaea	Bong.	28/08/2013	Serra do Cipó	19°17'	43°35'	1215	15	4	12
Vochysia thyrsoidea	Pohl	29/09/2013	Serra do Cipó	19°17'	43°35'	1263	10	6	25

## **Appendix S4**

Conservative extrapolated number of viable seeds used as correction factors for germination percentages of seeds which germinated less than 70% and lacked viability tests:

Таха	Conservative estimation of viable seeds	Number of inferences
Bromeliaceae		3
Dyckia	85	2
Encholirium	86	1
Cactaceae	97,3	1
Eriocaulaceae	85,6	11
Lythraceae	85,0	1
Melastomataceae		
Melastomeae	67,4	12
Miconieae	70,9	21
Microlicieae	42,0	17
Poaceae		
Seeds with embryo*	83,0	4
Unsorted seeds	69,5	2
Velloziaceae	95,0	2
Verbenaceae	68,2	3
Total		77

\* Empty seeds from these Poaceae populations were excluded prior to the germination experiment. Therefore, correction for these populations was made based on conservative value of viable seeds among seeds with embryos.