Universidade Federal de Minas Gerais
Instituto de Ciências Biológicas
Departamento de Ecologia
Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

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Research bias and scientific shortfalls in seed ecology literature compromise conservation of a megadiverse flora

Orientador: Prof. Dr. Fernando Augusto Oliveira e Silveira
Co-orientador: Dr. Alberto López Teixido

Fevereiro/2015
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Dissertação apresentada ao Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais como requisito parcial para a obtenção do título de Mestre em Ecologia.

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Abstract

Research biases are persistent issues in ecology, though their consequences for biodiversity conservation are often neglected. Bias presence across the literature accounts for knowledge gaps, since some *taxa*, geographic areas and species attributes remain overlooked. Deficient data on these attributes hamper accurate predictions of species responses to anthropogenic disturbances, resulting in inadequate conservation strategies. We evaluated research biases in the seed ecology literature in Brazil, a megadiverse country with endangered flora. Our focus on seed ecology lies in the paramount importance of seeds for *ex situ* and *in situ* conservation. We hypothesized that (1) the uneven distribution of Brazilian research institutions involves a geographic bias; (2) economic and ecological importance of some species entails a phylogenetic bias; and (3) these species generally have fleshy fruits and biotic dispersal, thus creating an ecological bias. Our data sources were both the Scielo database and the Web of Science. We analyzed geographic, phylogenetic and ecological biases, and generated a Kernel density map. Across 847 papers, we found that seed ecology research was geographically biased. The highest study densities were recorded in the Atlantic Rainforest and the Cerrado. *Taxa* with economic and ecological importance were overstudied, resulting in a phylogenetic bias. Likewise, we detected that threatened species were understudied. We also detected an ecological bias as tree, fleshy-fruited and biotic-dispersed species were overstudied. Overall, research biases and knowledge gaps in seed ecology result in negative implications for conservation, as it may limit the predictions about Brazilian flora responses to disturbances and adequate biodiversity management.

Key words: angiosperms; Brazil; ecological bias; geographic bias; Hutchinsonian shortfall; knowledge gaps; phylogenetic bias; threatened species

Resumo

Vieses nas pesquisas em ecologia são assuntos persistentes, embora suas consequências na conservação da biodiversidade sejam negligenciadas. A presença de vieses na literatura contribui para lacunas de conhecimentos, pois alguns *taxa*, áreas geográficas e atributos de espécies carecem informações. A ausência do conhecimento desses atributos dificulta previsões da resposta das espécies frente às perturbações antropogênicas, resultando em estratégias de conservação inadequadas. Avaliamos vieses na pesquisa em ecologia de sementes no Brasil, um país megadiverso com biodiversidade ameaçada. Nosso foco em ecologia de sementes deve-se a sua importância para a conservação *ex situ* e *in situ*. Hipotetizamos que (1) a distribuição desigual das instituições de pesquisa brasileiras promovem vieses geográficos; (2) a importância econômica e ecológica das espécies resultam em vieses filogenéticos; e (3) essas espécies, geralmente, possuem frutos carnosos e dispersão biótica, produzindo vieses ecológicos. Usamos as plataformas Scielo e Web of Science para construir nossa base de dados. Analizamos vieses geográficos, filogenéticos, ecológicos e geramos um mapa Kernel de densidade. Encontramos que a pesquisa em ecologia de sementes foi enviesada geograficamente. As maiores densidades de estudos foram registradas na Mata Atlântica e Cerrado. *Taxa* com importância econômica e ecológica foram sobre-estudados, resultando em vieses filogenéticos. Igualmente, detectamos que espécies ameaçadas são subestudadas. Encontramos também vieses ecológicos, pois árvores com frutos carnosos e dispersão biótica foram sobre-estudadas. Vieses e lacunas de conhecimento na pesquisa em ecologia de semente resultam em implicações negativas na conservação, pois limitam prever as respostas da flora brasileira aos distúrbios e manejo adequado da biodiversidade.

Palavras-chave: angiospermas; Brasil; lacunas de conhecimento; déficit Hutchinsoniano; viés ecológico; viés filogenético; viés geográfico; espécies ameaçadas

Introduction

Research biases are persistent issues in ecology, though their consequences for biodiversity conservation are often neglected. The distribution of biological knowledge is generally biased to certain taxa, environmental domains and geographic sites (Clark & May 2002, Hortal et al. 2008, Martin et al. 2012). Geographic research biases occur mainly because studies are costly in time and resources, but also because selection of field sites is influenced by biological characteristics (such as high biodiversity regions) and a wide array of financial and institutional constraints (Stocks et al. 2008, Martin et al. 2012). In this regard, the museum (Ponder et al. 2001) and botanist effect (Moerman & Estabrook 2006) were developed to explain research concentration in some areas. Hence, for historical reasons of efficiency, logistic and convenience, geographic research biases are the most intensively researched forms of sampling bias in nature (Werneck et al. 2011, Schmidt-Lebuhn et al. 2013). Geographic research biases permeate several fields of ecological literature such as invasion ecology (Pysek et al. 2008), selection of nature reserves (Bini et al. 2006, Pinto & Bini 2008) and distribution of biodiversity knowledge (Nelson et al. 1990, Kress et al. 1998, Hopkins 2007).

Non-geographic biases are also common in the ecological literature. Phylogenetic or taxonomic bias is an overall trend (Clark & May 2002) which is especially relevant in invasion ecology studies (Pysek et al. 2008, Jeschke et al. 2012). Ecological research can also be biased towards species traits (i.e. ecological bias), although it has received less attention (see Schmidt-Lebuhn et al. 2013). Altogether, both geographic and non-geographic biases prevent a full understanding of the biodiversity knowledge and, consequently, have profound implications for systematic conservation planning, selection of reserve areas and management of forces that cause habitat loss (i.e., deforestation, species invasion, mining, urbanization and infrastructure development; Jennings 2000, Williams et al. 2002, Nemésio et al. 2013, Schmidt-Lebuhn et al. 2013). Moreover, the presence of biases in the ecological literature accounts for knowledge gaps, since some subjects are overstudied while others remain overlooked.

Knowledge gaps on biodiversity are exemplified by the Linnean and Wallacean shortfalls. The Linnean shortfall (Brown & Lomolino 1998) is a concept that implies that many world species have not been described yet. The Wallacean shortfall (Lomolino 2004), in turn, sustains that the geographic distribution of the described species is poorly understood. Inadequate knowledge about species richness and distribution is a strong constraint for biodiversity management, because planning of nature reserves and other conservation strategies, such as restoration ecology practices and red lists, are performed considering this information (Jennings 2000, Clark & May 2002, Sousa-Baena et al. 2014). Consequently, studies relative to research biases and information gaps developed methodological analyses both to evaluate the uneven sampling effort in biodiversity databases and to increase the reliability of these records and their use in conservation actions (Ponder et al. 2001, Pardo et al. 2013, Sousa-Baena et al. 2014). In addition, gap analyses for identifying biodiversity elements (habitat types and species) not included in protected areas are vital for the development and implementation of systematic conservation planning (Burley 1988, Rodrigues et al. 2004, Habel et al. 2013). Although it is well recognized that the Linnean and Wallacean shortfalls can prevent implementation of effective conservation actions (Cardoso et al. 2011), little is known about the lack of information on the attributes that influence fundamental and realized niches of species (i.e. the Hutchinsonian shortfall, Mokany & Ferrier 2011) and its impacts on conservation biology. Deficient data on species attributes hamper accurate predictions on changes in species occurrence and abundance based on their attributes and interactions with other species resulting from climate change, habitat loss, fragmentation and exotic species invasion (Mokany & Ferrier 2011). These global change drivers lead to biodiversity loss, which is increasingly higher in the tropics, where most species occur (Collen et al. 2008, Dirzo et al. 2014, Duputié et al. 2014).

Here, we evaluated research biases in the seed ecology literature in Brazil, a megadiverse country. Brazil has a huge territorial extension (8.5 million Km^2) that creates pronounced geographic, climatic and biodiversity gradients. Nearly 20% of 1.5 million species described in the world occur in Brazil, bringing it to the leading position among the 17 megadiverse countries (Mittermeier et al. 1997, Giulietti et al. 2005, Lewinsohn & Prado 2005, see also Ministry of Environment 2002). Its native flora has 33,885 terrestrial plant species, comprising 31,162 angiosperms distributed in 235 families (Forzza et al. 2012, Brazilian Flora Species List 2014). Biome diversity is another conspicuous element of Brazilian landscape. In addition to the largest tropical forest in the world, the Amazon forest, Brazil is home of two major biodiversity hotspots, the Cerrado and the Atlantic Rainforest (Mittermeier et al. 1999, 2004, Myers et al. 2000). Hence, conservation of Brazilian floristic megadiversity is of global importance (Ferreira et al. 2014, Soares-Filho et al. 2014). Currently, as databases on species diversity and distribution are becoming increasingly available (Brazilian Flora Species List 2014, Sousa-Baena et al. 2014), we can also test for the first time whether the Hutchinsonian shortfall is evenly distributed among biomes and plant clades.

Our focus on seed ecology is due to the paramount importance of seeds. Examples include *ex situ* conservation initiatives such as the Millenium Seed Bank, which holds the largest wild seed collection in the world (DeBolt & Spurrier 2004). In addition, Millenium Seed Bank works with *in situ* conservation through restoration ecology practices. Seed bank projects together with management at conservation sites help to disentangle the mechanisms required for biome restoration and biodiversity preservation (Merritt & Dixon 2011). Besides, seed dispersal knowledge is critical for biodiversity management, since such an information subsidize conservation projects in climate change, habitat restoration, population viability analysis, land planning (systematic conservation planning) and invasive species (Galetti et al. 2013, Driscoll et al. 2014). Seed-based techniques, as management of seed dispersal, seed rain and using of soil seed banks assist many restoration projects in Brazilian Atlantic Rainforest (Rodrigues et al. 2009). Additionally, information about seed ecology may contribute to the understanding of the fundamental and realized niches of species. This knowledge helps to manage those plant communities threatened by anthropogenic disturbances and climate change effects. Overall, this may overcome the Hutchinsonian shortfall and assist conservation projects (Mokany & Ferrier 2011). Therefore, understanding research bias and knowledge gaps in seed ecology research will benefit both *ex situ* and *in situ* conservation initiatives.

Scientific publications discuss knowledge biases and gaps in several areas of conservation biology. Brazil has continental dimensions, a megadiverse flora and both uneven population and research institution distribution. This scenario favors the occurrence of research bias since, generally, researchers tend to study their surrounding environments and groups of species which have economic and ecological importance. Therefore, we hypothesize that seed ecology research in Brazil is geographically, phylogenetically and ecologically biased. These biases, especially the ecological one, contribute for Hutchinsonian shortfall and may compromise the conservation of a megadiverse flora. Hence, our study specifically aimed to review the seed ecology studies of Brazilian angiosperms and test the following hypotheses: 1) the Atlantic Rainforest and Cerrado are overstudied because the majority of Brazilian research institutions are located in these hotspots; 2) species with economic and ecological importance are overstudied, resulting in a phylogenetic bias; and 3) species with economic and ecological importance generally have fleshy fruit and biotic dispersal, which suggests that these traits may be overrepresented.

Material and Methods

Data source

Our primary data sources were both the Scielo database (www.scielo.br) and the Web of Science (hereafter, WOS; www.webofknowled.com) wherein papers were surveyed between August and December 2013. In the Scielo database we examined all studies dealing with at least one topic on seed ecology across all volumes available from 18 journals (Appendix S1). The Scielo database comprises the most important Brazilian journals and provides open access to papers published in Portuguese and English. In WOS, we searched for “seed” and “Brazil” excluding journals examined in the Scielo database to avoid redundant records. We used both databases because some Brazilian journals included in the Scielo platform are still absent in the WOS database. Therefore, searching in both databases was important to reach the largest potential number of papers published to date. We searched for seed ecology papers by looking at title, keywords and abstracts in both databases.

Each paper was classified into one of the following topics: 1) seed germination (abiotic and/or biotic control of germination, hormonal control, allelopathy, reserve mobilization, fire effects on germination and seed technology); 2) seed banks (seed longevity, seed bank dynamics, seed storage and dormancy cycles in soil); 3) seed dormancy (dormancy kind determination and dormancy overcome in the wild); 4) seed dispersal (frugivory, seed dispersal effectiveness and gut passage effects); 5) seed predation (pre-dispersal and post-dispersal seed predation); and 6) seed removal (when seeds were removed but the lack of animal identity prevents determining seed fate; Vander Wall et al. 2005). We excluded data from cultivated, ornamental, naturalized, exotic and invasive species, thereby restricting our sample to native species included in the Brazilian Flora Species List (2014). The Brazilian Flora Species List (2014) is a recently developed database and constantly updated by a group of more than 300 plant taxonomists. This database aims to georeference all plant species in Brazil and provides reliable information of species richness across biomes and plant clades. Likewise, descriptive studies relative to the phenology, phytochemistry, seed morphology, studies in agroecosystems and studies dealing with species composition in seed rain and seed banks were not included in this review. Reproductive biology studies were included only when seed germination was investigated. These sampling criteria aimed to build our database on studies strictly related to seed ecology. Review studies (e.g. Zaidan & Carreira 2008) were also checked to find papers absent in our database.

In each paper, we assigned the kind of topic individually since one single species may have been assigned to multiple topics of research in one or several papers. Also, one single paper was used to study all species which showed research in at least one topic of seed ecology. Each relation between species and seed ecology topics in papers was defined as a single case. For each species we collected phylogenetic, ecological and biogeographic data. We also assigned the threat category, considering only vulnerable, endangered and critically endangered species following the National Flora Conservation Centre (CNCFlora 2014), a reliable biodiversity and conservation database of the

Brazilian endangered flora, which considers the IUCN Red List criteria (IUCN 2014). For phylogenetic data, both nomenclature and classification followed APG III (2009). Nomenclature was checked against Brazilian Flora Species List (2014), The International Plant Names Index (IPNI 2014) and Tropicos Database (2014) to avoid synonymies. For ecological data, we recorded different plant functional traits (*sensu* Violle et al. 2007), including: growth-form (herbaceous, shrub, tree, palm, epiphyte or climber), fruit type (dry or fleshy) and dispersal syndrome (abiotic or biotic) (Pérez-Harguindeguy et al. 2013). We considered unassisted, wind-dispersed and water-dispersed syndromes as abiotic dispersal, whereas ballistichory, hoarding, endozoochory and exo-zoochory were considered as biotic dispersal. Plant functional trait data were collected from Brazilian Flora Species List (2014) and specialized plant taxonomy and morphology literature (e.g., Zanoni 1967, Steyermark et al. 1999, Barroso et al. 1999). For biogeographic data, we obtained geographic coordinates provided by the authors for each studied species. When precise coordinates were not available we used the coordinates of the studied site and, when both information were lacking, we excluded the study from the analyses of geographic bias. We also recorded the Brazilian biome in which the study was conducted: Amazon forest, Caatinga, Pampas, Cerrado, Atlantic Rainforest and Pantanal (see Ferreira et al. 2014 for details). When information on the biome was not provided in the paper we plotted the study area geographic coordinates in Brazilian biome shapefile to define it. Lastly, we recorded whether the study was conducted inside or outside of a protected area. The protected areas considered only the conservation units belonging to the national system of protected areas in Brazil (Silva 2005).

Data analyses

1. Geographic bias

To determine research bias and knowledge gaps in seed ecology across Brazilian biomes, a Kernel density raster layer (e.g. Yang et al. 2013) was elaborated to access the density of seed studies, with a resolution of 0.0083° (~1km) using the Spatial Analyst toolbox in ArcGis v9.3 (ESRI, Redlands, CA, USA). This approach was used to obtain a better representation of areas with excessive concentration of studies. The layer was used to understand the distribution of seed ecology research across Brazilian biomes and to disentangle between overrepresented and underrepresented biomes. To visualize the differences between density values for each biome we generated 50,000 uniformly random points for entire country and calculated the mean Kernel density for each biome. The variance in mean Kernel density values between biomes was accessed by means of a generalized linear model (GLM) followed by multiple comparisons of means using the MULTICOMP v1.3-8 package in R statistical package version 3.1.1 (R Development Core Team 2010). The studies and their analyzed topics were separated by biomes. Seed ecology research distribution inside and outside conservation units was also analyzed. A null model was performed with 999 randomizations by means of the "sample" function using the R statistical package version 3.1.1 (R Development Core Team 2010) and a bicaudal test (95% confidence interval) was performed to test significant differences of research distribution in these areas.

2. Phylogenetic bias

To determine phylogenetic bias we firstly recorded the Brazilian angiosperm total richness as well as the richness per families and genera following Brazilian Flora

Species List (2014). We only considered families and genera showing any seed ecology study according to the criteria explained across the literature. We collected these data between June and December 2014. Then, we obtained the percentage of the observed species richness (i.e., studied richness) per plant family and genus, and the percentage of the expected species richness (i.e., actual richness) of each family and genus over the total richness of Brazilian angiosperms. To determine significance of phylogenetic bias the percentage of studied species was regressed against percentage of family and genus richness and a regression slope was calculated. Departure of the slope from 1 indicates a bias in the relationship between percentage of studied species and percentage of family and genus representativeness over Brazilian total richness. For example, a slope >1 would indicate a positive bias, i.e., a disproportionate increase in studied species percentage when increasing families and genera richness, whereas a slope <1 would indicate a negative bias, i.e., a disproportionate decrease in studied species percentage when increasing families and genera richness. Comparisons between slopes were studied by means of *t*-tests (Zar 1999).

For each family and genus we calculated a relative bias rate (BR_i, see Nemésio et al. 2013) between the percentage of studied species and the percentage of representativeness of that family or genus in Brazil using the formulae:

(1) $BR_i = a_i / b_i$

(2) $BR_i = (b_i / a_i) \times (-1)$

where a_i and b_i are the percentage of studied species and the percentage of representativeness in Brazil, respectively, of family or genus *i*. When the values of a_i were higher than the values of b_i we used (1) and when the values of b_i were higher than the value of a_i we used (2), thus showing an equivalent graphical representation between positive and negative values (Nemésio et al. 2013). Null values entail equivalence between the percentage of studied species and the percentage of representativeness of any particular family or genus in Brazil. Positive values mean greater, and negative values lower, percentage of studied species than percentage of representativeness of any particular family or genus.

We also determined phylogenetic bias for threatened species. The percentage of threatened studied species per plant family was regressed against the percentage of threatened species across plant families and a regression slope was calculated. We followed the same pattern for departure of the slope from 1 used above. Comparisons between slopes were studied by means of *t*-tests (Zar 1999).

3. Ecological bias

We also determined the existence of bias in plant functional traits (fruit and dispersal type) of species in our database. Null models were performed with 999 randomizations by means of the "sample" function using the R statistical package version 3.1.1 (R Developmet Core Team 2010) and a bicaudal test (95% confidence interval) to test significant differences of data distribution in these areas.

Results

Data set

We found 574 articles in the Scielo database comprised between 1976 and 2013, and 868 articles in WOS platform from 1983 to 2013. After excluding 595 studies that did not meet our sampling criteria, our database comprised 847 papers (Fig. 1) and 5322 cases, relationships between species and seed ecology topics. The 10% of papers (n =

88) did not ever mention the study area municipality or the geographical coordinates, so they were not included in the geographical bias analysis.

From the 90's there was an increase in the number of seed ecology studies as well as the topics researched (Fig. 1). The most studied topics were seed dispersal (47%), seed germination (20.5%) and seed predation (13.9%). The largest number of studies, on average, was found for seed dispersal (65.7 studies/year), germination (28.6 studies/year) and predation (19.4 studies/year).

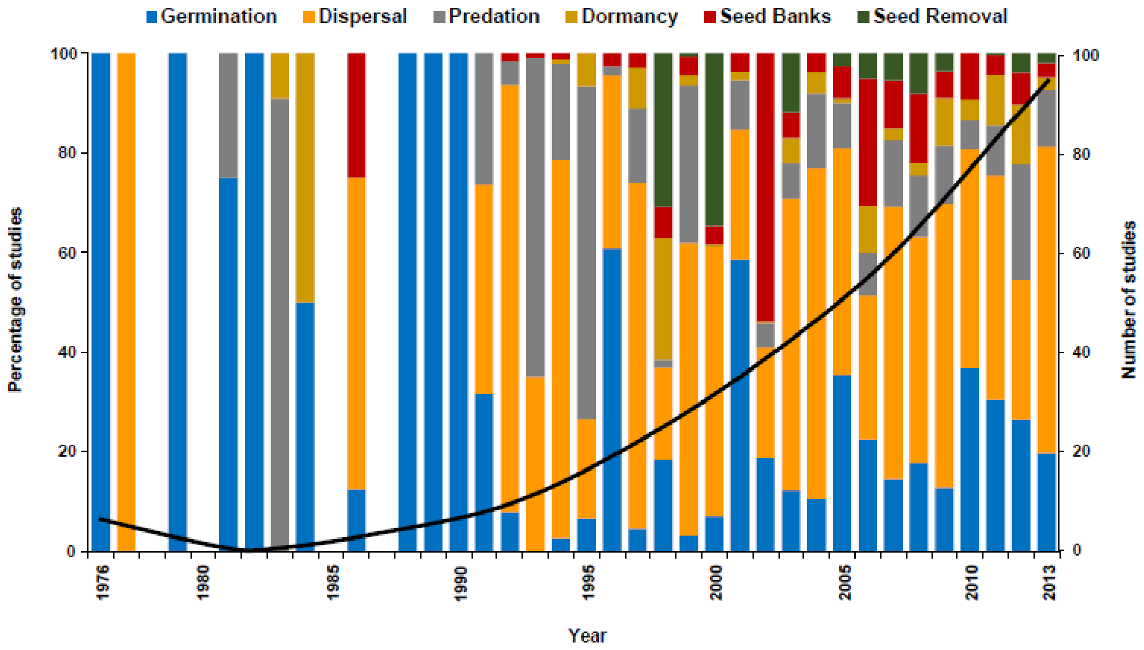

Figure 1. Temporal variation in seed ecology topics of Brazilian angiosperms reviewed in Scielo and Web of Science platforms between 1976 and 2013. The line represents the best fit between a number of published articles and years: $y = 0.097x^2 - 386x + 382799$, $R^2 = 0.91$.

Geographic bias

The distribution of research effort in seed ecology was geographically biased. There was a high research density in some biomes whereas other ones showed knowledge gaps (Fig. 2). The highest mean Kernel density was recorded in the Atlantic Rainforest, followed by the Cerrado and the Pantanal, whereas the Pampas showed the lowest mean Kernel density. Overall, the Amazon forest had a low mean Kernel density, but a high research density in three regions (Fig. 2). Relative to protected areas, most studies were conducted within conservation units ($P < 0.001$).

Seed germination was the dominant topic in all biomes (range: 34-64%) except in Pantanal, wherein seed dispersal was the most studied topic (45%, Fig. 2). Seed dispersal was also the second most studied topic in Atlantic Rainforest (29%), Amazon (26%) and Cerrado (18%). Conversely, seed removal was the topic receiving the lowest number of studies in all Brazilian biomes (range: 0-5%) except in Pantanal, where seed dormancy did not receive any study.

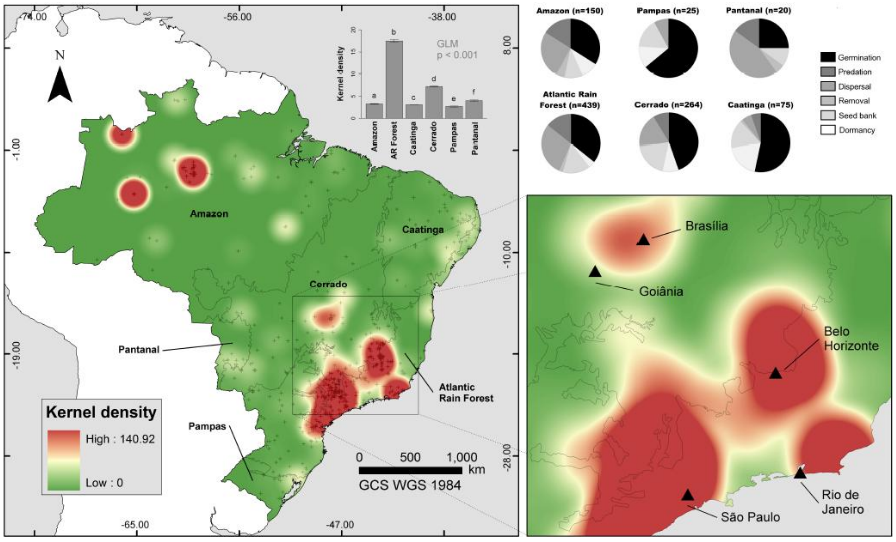

Figure 2. Kernel density for studied angiosperm species in Brazilian biomes. The panel located above on the right shows the study number and the proportion of each topic per biome. In the map, each cross refers to a single case. The graph shows significant differences in the mean Kernel density for seed ecology studies per biome in Brazil. Columns denote the means, different letters indicate significant differences among biomes and bars the standard errors (GLM, family = poisson, df = 5, deviance = 144789, P < 0.001). This map was created using biomes shapefile from Brazilian Ministry of the Enviroment and ArcGis 9.3 (ESRI).

Phylogenetic bias

Overall, we found 40 orders, 123 families, 649 genera and 1648 studied species for at least one topic of seed ecology in Brazil (Table 1).

Table 1. Number and percentage of existent and threatened families, genera and species of angiosperms that have been studied in at least one topic of seed ecology in Brazil.

Research	Families		Genera		Species	
	Existent[a] (%)	Threatened[b] (%)	Existent[a] (%)	Threatened[b] (%)	Existent[a] (%)	Threatened[b] (%)
Studied	123 (52.3)	23 (16.5)	649 (21.9)	54 (7.8)	1648 (5.0)	74 (3.4)
Not studied	112 (47.7)	116 (83.5)	2314 (78.1)	631 (92.2)	31084 (95.0)	2044 (96.6)
Total	235 (100)	139 (100)	2963 (100)	685 (100)	32732 (100)	2118 (100)

[a] *Total data for the last row were collected according to Brazilian Flora Species List (2014)*
[b] *Total data for the last row were collected according to CNCFlora*

We did not detect any significant phylogenetic bias in seed ecology research at family-level (Fig. 3A). However, we found a significant positive phylogenetic bias at genus-level. (Fig. 3B).

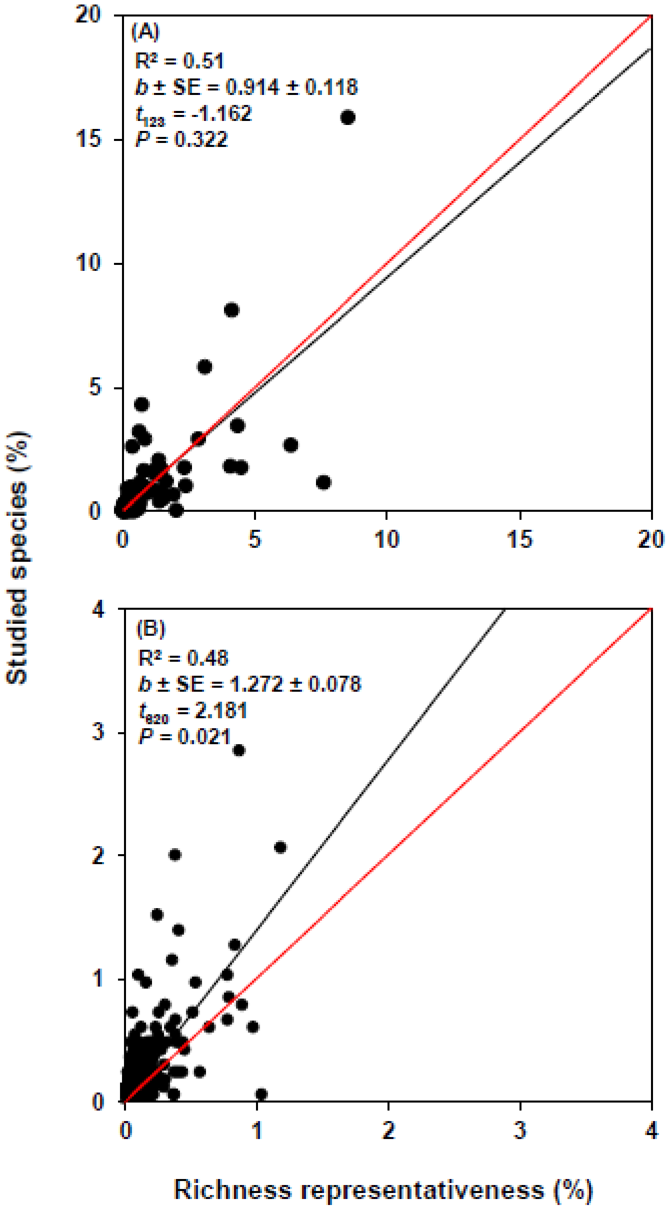

Figure 3. Relationship between the percentage of studied species in seed ecology across plant families (a) and genera (b) and family and genus richness representativeness over total richness of Brazilian angiosperms.

We also detected a significant negative bias for the analysis of threatened species (Fig. 4).

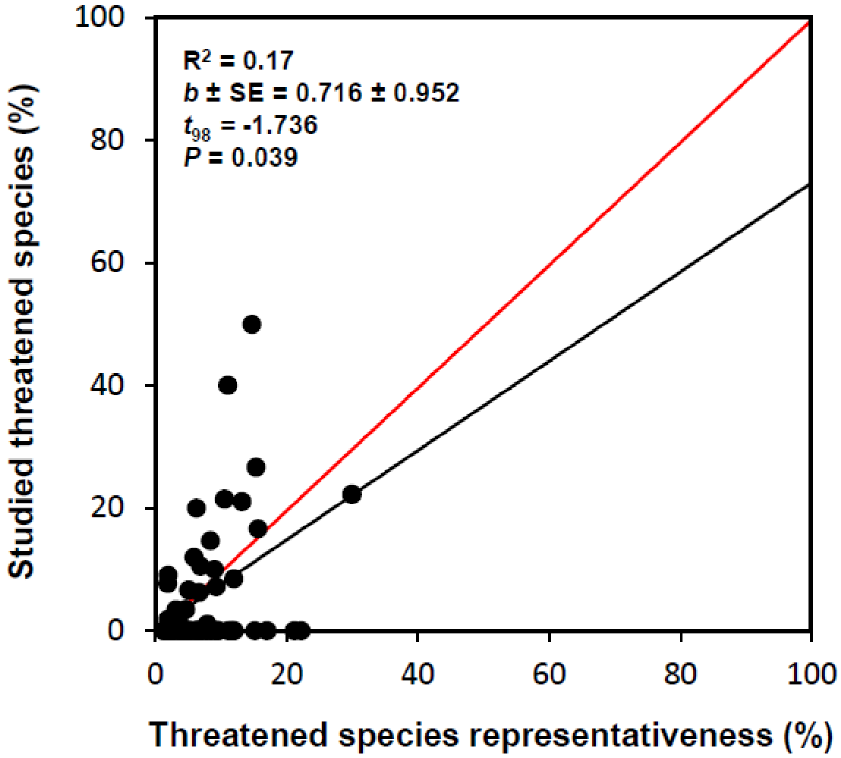

Figure 4. Relationship between the percentage of studied threatened species in seed ecology across plant families and threatened species representativeness across plant families in Brazil.

Some plant families and genera were highly over or underrepresented in the literature as they have shown high (very positive) or low (very negative) relative bias rate, respectively (Fig. 5). For plant families, Stemonuraceae and Muntigiaceae showed the highest relative bias rates (19.5) whereas Cyperaceae showed the lowest one (-33.4). In relation to genera, 78 of them, which represent about 12% of studied genera, showed the highest relative bias rate (19.8). However, only a few genera showed low relative bias rates: *Paepalanthus* (-16.9), *Rhynchospora* (-7.3), *Serjania* (-6.0), *Turnera* (-5.9) and *Hyptis* (-5.9).

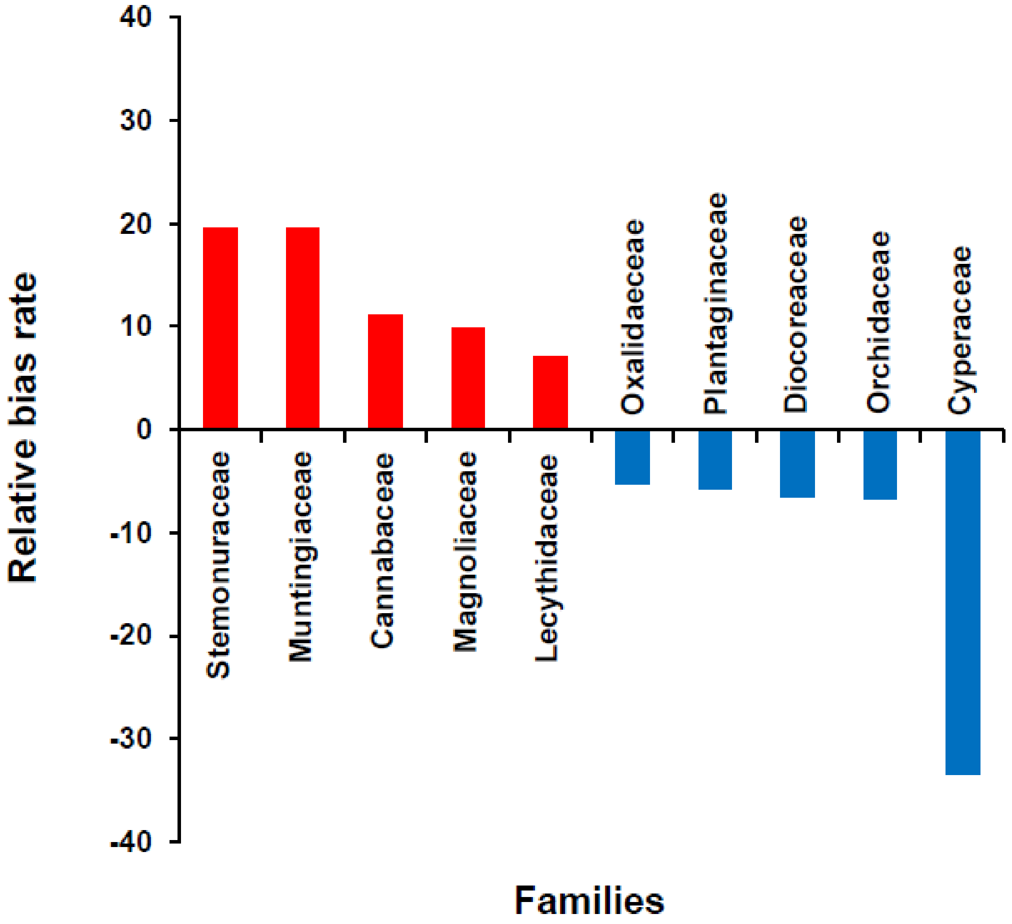

Figure 5. Relative bias rate for plant families which showed the higher and lowest values in seed ecology literature of Brazilian angiosperms.

Ecological bias

We recorded studies in 1026 trees, 350 shrubs, 196 herbs, 121 climber, 49 palm trees, 10 epiphyte and two aquatic plant species. Tree species were overstudied and herbs understudied as the Brazilian flora has 12,941 species of herbs and 8,167 species of trees (Brazilian Flora Species List 2014). Regarding fruit type and dispersal syndrome, we recorded 875 species with fleshy fruits and biotic dispersal, 572 species with dried fruit and abiotic dispersal and 201 species with dried fruit and biotic dispersal. Fleshy-fruited species were disproportionately overstudied compared to dry-fruited species (*P* = 0.006), as well as biotic seed dispersal compared to abiotic (*P* < 0.001).

Among the 1648 species found on our review, 1057 received studies in only one seed ecology topic, 396 were studied in two topics, 130 in three topics, 44 in four topics, 17 on five topics and only 4 species received studies in all evaluated topics. The distribution of seed ecology studied topics across angiosperms lineages revealed that seed germination and seed dispersal predominated, while the other topics received fewer research (Fig. 6).

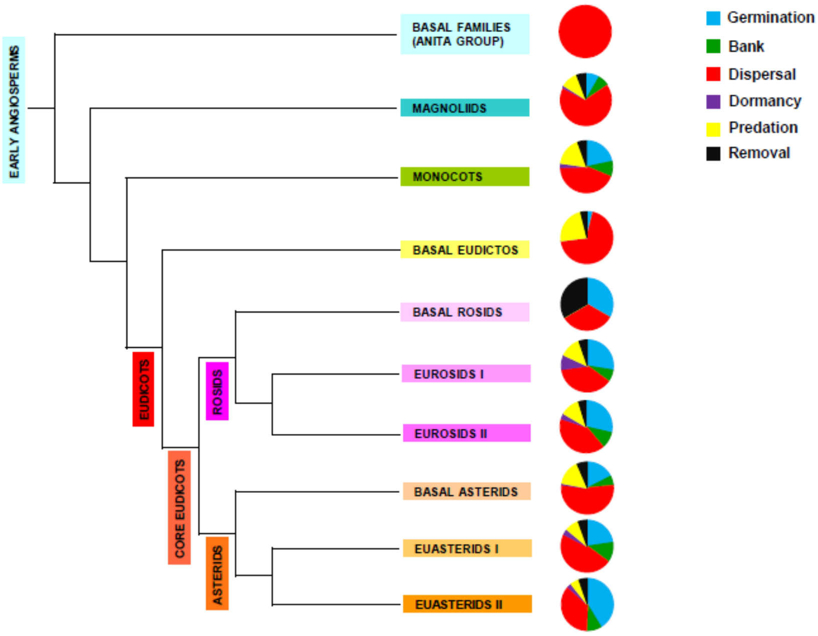

Figure 6. Seed ecology studied topics of Brazilian angiosperms across angiosperms lineages. Phylogeny follows APG III (2009).

Discussion

Our study found research bias together with some knowledge gaps in seed ecology literature in a megadiverse flora with high level of endemism and threatened species. Overall, we verified our hypotheses confirming that seed ecology research in Brazil is geographically, phylogenetically and ecologically-biased, so a high number of biomes, species and traits deserve further attention. Although we did not detect any phylogenetic bias when analyzing families, we did find a phylogenetic bias for genera. Most interestingly, we found that some families and genera are highly under or overstudied and that threatened species lack exhaustive research in terms of seed ecology, thus contributing for conservation gaps. We also detected that Brazilian seed ecology research was very focused in some biomes, despite all of them were studied. Finally, we found that only a few species, ecological and plant life history traits are well-known and studied. Our results support the existence of knowledge bias and an inadequate distribution of studies and resources in seed ecology research. These findings have implications for Brazilian angiosperm conservation and outline purposes and targets for future research. We discuss our results in relation to these assumptions, thus suggesting the most important upcoming research lines in seed ecology and proposing conservation strategies for the highly diverse and threatened Brazilian angiosperm flora.

Assessment of research bias

Biases in ecological research have been documented in a high number of studies over the world. For example, Martin et al. (2012) reported a high over-representation of protected areas, temperate deciduous forests and rich countries across more than 2,500 global ecological studies. Conservation studies in terms of selection of protected areas and biological invasions are also biased for countries with high per capita income, but not necessarily megadiverse (Pinto & Bini 2008, Pysek et al. 2008). Pysek et al. (2008) also showed that invasive species with the highest impact on native ones are the best studied. The historical process of dung beetles species recorded in Spain showed spatial and environmental biases of survey, which interfere in the observed environmental niche of species (Hortal et al. 2008). In Brazil, some studies also showed bias in their results. In a conservation biology survey, most studies occurred in the Amazon and Atlantic Rainforest biomes (Grelle et al. 2009). In the Amazon forest, endemism centers were correlated with research sampling effort and the peak of knowledge of biodiversity was significantly associated to the areas where most collections occurred (Nelson et al. 1990, Kress et al. 1998, Hopkins 2007). For the Atlantic Rainforest, a geographic bias was reported since the highest endemic angiosperm richness was related to the main research centers (Werneck et al. 2011). However, all these biases are related to Linnean and Wallacean shortfalls but, as far as we are concerned, our study is the first to show geographic and non-geographic bias on the attributes that influence fundamental and realized niches of species, the so-called Hutchinsonian shortfall (see Mokany & Ferrier 2011).

We detected a high density of studies in northern and southeastern areas of Brazil (Fig. 2). This result is likely related to botanist and museum effects (Ponder et al. 2001, Moerman & Estabrook 2006), which explain the highest number of studies in certain areas due to historical reasons of efficiency, logistics and convenience in research (see also Werneck et al. 2011 for Brazilian endemic angiosperms). This assumption is closely related to the high concentration of studies in three regions of the Amazon, as well as the Atlantic Rainforest and Cerrado biomes, as they are the main biomes in the Brazilian northern and southeastern areas, where most research centers are located. In agreement with this, the area comprising the most part of the Atlantic Rainforest, which was most intensively studied, also includes the highest number of Brazilian research institutions. We also found a geographic bias in three Amazonian sites corresponding with the largest cities, research centers and conservation units, as pointed out by other studies in this biome (Nelson et al. 1990, Kress et al. 1998, Hopkins 2007). In addition, the existence of many inaccessible areas in the Amazon biome constraints research distribution and contributes to the higher density of studies in these three main sites. However, the total area of the large Amazon forest was responsible for the low mean Kernel density across this area when compared to others (Fig. 2). Interestingly, we detected a positive geographic bias for protected areas, which involves that Brazilian conservation units are important sources and natural laboratories for seed ecology studies. This result agreed with a global pattern. Nature reserves are relevant for research development over the world, since a review evaluating 2573 terrestrial ecological papers in the whole world between 2004 and 2009 found that 63% of study sites were situated in protected areas (Martin et al. 2012).

The uneven selection of species for the conducted studies is responsible for phylogenetic bias in different research areas. In biological invasion research, alien species, which are responsible for economic losses, are more researched than other alien species (Pysek et al. 2008). Phylogenetic bias may also be due to conservation matters, as charismatic and endangered species are more frequently studied (Pinto & Bini 2008). We found that selection of the most studied species was influenced by their ecological and economic importance, besides risk of extinction. The choice of species with these characteristics did not generate phylogenetic bias in seed ecology research at family level. This involves that there is an equivalent proportion between the percentage of studied species across plant families and the percentage of representativeness of those families over the total richness of Brazilian species. In other words, richer plant families were proportionately more studied, generating less information gaps and positive implications for conservation. However, we detected a positive phylogenetic bias at genus level, which means that there is not an equivalent proportion between the percentage of studied species across genera and the percentage of representativeness of those genera over the total richness of Brazilian species. Despite the threat status accounts for the selection to study species, we found negative phylogenetic bias for threatened studied species. This reveals that the percentage of threatened species studied in seed ecology research is not proportional to the percentage of threatened species in plant families. Hence, the number of threatened species studied does not increase in some families with many endangered species. Presence of these biases in seed ecology research produces information gaps and negative implications for conservation, which will be discussed later in this study.

The highest relative bias rate was found for Stemonuraceae (*Discophora guianensis*) and Muntingiaceae (*Muntingia calabura*), because they are monospecific families which presented at least one study on the ecology of their seeds. However, these families represent a small fraction over total richness of Brazilian angiosperms. The high relative bias rates found for Cannabaceae, Magnoliaceae and Lecythidaceae may be relative to their species contribution to the feeding ecology of many studied frugivores, since the consumption of their fruits and seeds are frequent. Therefore, due to a national tradition on seed dispersal ecology, the species of these families showed many studies on seed dispersal, removal and predation (e.g. Galleti & Pedroni 1994, Boubli 1999, Pizo & Oliveira 2000, Mannheimer et al. 2003, Jerozolimsky et al. 2009, Barnett et al. 2012). In addition, due to ecological importance of these families, they received many studies in other seed ecology topics such as germination, banks and dormancy, which also contribute for the high relative bias rate. The economic importance of *Bertholletia excelsa* (Lecythidaceae), which provides the main non-timber product extraction for export in the Amazon (Silva et al. 2009), also contributes to the high studies number and bias rate for this family. Relative to plant genera, 78 of them showed the highest values, as they are monospecfic and bispecific groups with at least one study in seed ecology topics. Nevertheless, they represent little over the total richness of Brazilian angiosperms.

Relative to ecological bias, our results demonstrate that most of seed ecology studies are carried out with tree, fleshy fruits and biotic seed dispersal species. This result may be explained by the high number of studies on feeding ecology found in our review and agrees with a strong national tradition on seed dispersal ecology (e.g. Galleti & Pedroni 1994, Boubli 1999, Pizo & Oliveira 2000, Mannheimer et al. 2003, Jerozolimsky et al. 2009, Barnett et al. 2012). In feeding ecology studies, some plant species comprising the animals' food sources are reported. Most of these plants have fleshy fruits attractive to fauna who remove, disperse and/or predate seeds. Therefore, feeding ecology studies have a greater contribution to the knowledge of seed removal, dispersal, and predation than over other seed ecology topics (Peres 1993, Galleti et al. 1997, Guimarães Jr & Cogni 2002, Pizo 2004, Guimarães Jr et al. 2005). Hence, the feeding ecology studies could be responsible for the ecological bias detected.

Implications for conservation in Brazil

Brazil is a world leader in floristic diversity and home of the Earth's largest tropical rainforest, the Amazon, as well as of two biodiversity hotspots, the Cerrado and the Atlantic Rainforest (Barthlott et al. 1996, Mittermeier et al. 1997, Myers et al. 2000). However, the Brazilian biodiversity is highly threatened due to human activities, culminating in habitat loss, fragmentation and species extinction (Brandon et al. 2005, Leal et al. 2005, Fearnside 2005, Overbeck et al. 2007, Carvalho et al. 2009, Joly et al. 2014). In addition, these human activities promote shifts in Brazilian environmental legislation and threaten protected areas wherein the last remnants of Brazilian biomes are preserved (Ferreira et al. 2014). Knowledge in seed ecology could help to understand how the Brazilian biodiversity will respond to these increasing anthropogenic pressures and offers opportunity to contribute for restoration of degraded sites. However, this research area shows some biases and knowledge gaps, which highlight and support the importance of increasing this research for conservation strategies.

The geographic bias in seed ecology literature of Brazilian angiosperms is responsible for knowledge gaps within and among biomes, resulting in negative implications for biodiversity conservation. This result shows that little is known about the seed ecology of angiosperms species in some Brazilian biomes such as the Amazon, Pampas and Caatinga (Fig. 2). Even in the well-studied Atlantic Rainforest and Cerrado, there are many information gaps, as only 123 of the 235 plant families of Brazilian angiosperms show seed ecology studies (Table 1). The lack of this knowledge limits the management of biodiversity, because seed ecology research generates knowledge about species germination, seed dormancy, seed banks, seed predation and seed dispersal that subsidizes *ex situ* and *in situ* conservation projects over world and in Brazil, which are extremely relevant for biodiversity saving. Thus, the biodiversity crisis faced by Brazil demands further research and knowledge on the seed ecology in this country, as this information could help mitigate and counteract this scenario.

Botanic gardens are involved with projects drawn to preserve flora biodiversity. Among these projects subsidized by botanic gardens and seed bank knowledge, one of the most ambitious is The Millenium Seed Bank, a worldwide seed collection program, which holds 18,000 wild plant species from 126 countries, the largest wild seed collection in the world (DeBolt & Spurrier 2004, Williams 2007). Studies on the seed resistance and longevity relative to storage conditions are vital for development of these projects (Probert et al. 2009). Our review found only 262 species that have studies in seed banks topic, which means that we have some seed storage knowledge for only 0.8% of Brazilian angiosperm species. Whereas the Brazilian biomes are being increasingly degraded through different anthropogenic activities and the amount of information about seed longevity becoming available, we thoroughly propose that it is urgent further development of this important research line aiming to contribute for genetic heritage preservation of Brazilian angiosperms in the Millenium Seed Bank Project. Some stored seeds are also used in habitats recovery because the objectives of the Millenium Seed Bank Project range from *ex situ* (seed banks) to *in situ* (habitat restoration) conservation practices.

Many others botanic gardens are practicing restoration ecology over the world (Hardwick et al. 2006). In this regard, botanic gardens play a relevant role in biodiversity conservation. Also, botanic gardens are essentials to mitigate climate change effects on biodiversity. Knowledge and data on plant systematics, distribution and physiology is relevant for managing the impacts of climate change, helping to identify most threatened plant species and habitats (Ali & Trivedi 2011).

Climate change significantly affects temperature, rainfall, fire regimes and soil moisture. These abiotic factors are critical drivers for seed dormancy (initiation, break), seed bank persistence in soil and germination (Walck et al. 2011, Ooi 2012). Improving our understanding in these mechanistic responses and adaptive capacity of species to climate change will provide a solid basis for improved predictions of future population distributions and risk of extinction. Thus, increased research in understudied biomes on key issues related to seed ecology, such as seed dormancy, banks and germination is needed to fully understand the plant responses to climate change. Besides, development and cultivation of functional groups of plants based on key life-history trait responses to changing environmental conditions will allow restoring disturbed and fragmented areas as well as knowing broader-scale predictions of species distribution and future persistence (Walck et al. 2011, Ooi 2012). In addition, understanding the dynamics of seed banks occurring in preserved and degraded sites allows us knowing the resilience of plant communities as well as their response to soil disturbances (Fagan et al. 2010, Salazar et al. 2012).

Likewise, knowledge about seed dispersal, removal and predation dynamics in remnant biomes could counteract the Brazilian biodiversity crisis. For example, knowledge of these seed ecology topics allows us understanding the plant-animal interactions in fragmented habitats with different characteristics such as area, harvest intensity, fauna preservation levels, levels of protection and connectivity (Guariguata et al. 2000, Silva & Tabarelli 2000, Fadini et al. 2009, Donatti et al. 2011). This information may contribute to biodiversity management by understanding how populations may be connected and species interact in a perturbed scenario.

Seed ecology research also offers useful information about *in situ* conservation projects, such as the restoration of degraded areas. A evaluation of where and how to collect seeds to promote ecological restoration of disturbed areas reported recommendations for herbaceous and woody species in areas of contrasting conservation values (Mijnsbrugge et al. 2010). Another study suggested alternative seed sourcing strategies for revegetation aiming to mitigate habitat fragmentation and climate change as drivers of biodiversity loss (Breed et al. 2013). Moreover, some reviews summarize the main findings and challenges for restoration in Brazilian hotspots biomes, such as Atlantic Rainforest and Cerrado (Rodrigues et al. 2009, Silveira et al. 2013). These studies show seed-based techniques as management of seed dispersal, seed rain and soil seed bank using to carry out restoration projects.

Our study also shows the importance of conservation units for seed ecology studies as most of them were conducted within these areas. The protected area network in Brazil is the largest of the world (WDPA 2014), which helps to conserve such a megadiversity and facilitates its survey. However, agriculture, mining and dam construction threaten the protected areas by means of shifts in the Brazilian environmental legislation (Ferreira et al. 2014, Soares-Filho et al. 2014). It is responsibility of the scientific community, environmental agencies and survey institutions to question these changes and demonstrate the importance of protected areas for biodiversity conservation and research development. However, it is relevant consider that concentration of seed ecology research in conservation units involves problems for conservation itself, since constraints the development of ecological theories and prevents conservation efforts in human-populated areas (Martin et al. 2012).

Considering the implications of geographic bias and knowledge gaps we suggest more political, economic and scientific investments in seed ecology research in Brazil to achieve a uniform geographical distribution of the studies. Although constant research in protected areas is required, it is essential to understand seed ecology in human-populated areas to develop preservation strategies specific to those areas and to try to carry out them rather than developing explicit theories in conservation areas (Martin et al. 2012). We also recommend to seed ecology researchers further studies in Cerrado and Atlantic Rainforest, which are biodiversity hotspots (Myers et al. 2000). However, it is critical to conduct a greater number of studies in biomes that have little survey, such as the Caatinga and Pampas to preserve their exclusive biodiversity and ecosystem services.

Pampas shows very high levels of floristic biodiversity, including endemisms and threatened species, but it has been long neglected by the government and by the scientific community as studies about the effects of disturbance on plant community and populations are scarce (Overbeck et al. 2007, Fidelis et al. 2008). The Caatinga shows high levels of flora biodiversity and endemism. Inappropriate land use has already caused serious environmental damage in this biome and conservation strategies are necessary to avoid further habitat loss and desertification, thus maintaining key ecological services and promoting the sustainable use of the regional natural resources (Leal et al. 2005).

Relative to phylogenetic bias, seed ecology studies revealed information gaps for total richness of Brazilian angiosperms (Table 1). However, the absence of a phylogenetic bias in terms of families may have positive implications for conservation. In this regard, knowledge is produced in a proportional manner, contemplating most of family species, which allows information generated by seed ecology research to subsidize conservation strategies for studied species. However, due to the negative bias found for some highly rich genera (e.g. *Paepalanthus*, *Rhynchospora*, *Serjania*), additional knowledge gaps are generated, resulting in negative implications for the establishment of conservation strategies. The analysis of threatened species also revealed knowledge gaps (Table 1) and a significant negative bias in seed ecology research. This is an unexpected and warning result for conservation since threatened species should be the most studied ones and preservation strategies of endangered biodiversity rely on species knowledge.

Regarding the ecological bias, tree species are overstudied whereas herbs and dry-fruited species are underrepresented in seed ecology research. Thus, seed ecology research has a disproportionate number of studies of tree species, which implies less knowledge on seed ecology of herbaceous species and other life-forms. The restoration of open habitats depends on the management of herbaceous species, so information gaps on seed ecology of this group of plants contribute to Hutchinsonian shortfall and may limit conservation projects of biodiversity.

Moreover, 1057 species showed studies in only one topic of seed ecology and four species presented studies in all seed ecology topics evaluated in this review. In angiosperms lineages, some seed ecology topics such as germination and dispersal are well studied, but others topics such as seed banks and seed dormancy received little attention. These biases and information gaps on seed ecology constraint the full understanding about environmental niche of many species and contribute to the Hutchinsonian shortfall. When the environmental niche of species is unknown it is difficult to predict the responses of plant communities to anthropogenic modification of landscape together with climate change. The results of our review indicate that further information is needed about the species seed ecology to forecast the biodiversity of Brazilian angiosperms that will adapt and survive in landscapes with increasing threats in the next fifty years. Lastly, preservation strategies for species depend on some knowledge, including seed ecology, so the lack of a full understanding on seed ecology also difficults the species biodiversity management.

Conclusions

Brazil is a megadiverse country with threatened biodiversity due to landscape perturbation and climate change caused by human activities. Knowledge on seed ecology topics may predict the responses of plant communities to disturbances and contributes to the understanding of the environmental niche of species (i.e. Hutchinsonian shortfall), which may assist many *ex situ* and *in situ* conservation projects developed to mitigate and overcome the Brazilian biodiversity crisis. However, our study found geographic, phylogenetic and ecological bias as well as knowledge gaps. Therefore, the lack of full information about species seed ecology results in negative implications for conservation, since it may limit the forecast about Brazilian flora responses in the future and the management of biodiversity.

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Appendix

Appendix S1. Number of seed ecology studies across the Scielo database journals. Numbers in brackets represent the total number of studies found for each journal.

Journal of Seed Science (116), *Revista Árvore* (87), *Acta Botanica Brasilica* (51), *Acta Amazonica* (44), *Brazilian Journal of Botany* (44), *Cerne* (35), *Planta Daninha* (35), *Brazilian Journal of Biology* (31), *Pesquisa Agropecuária Brasileira* (27), *Biota Neotropica* (23), *Brazilian Archives of Biology and Technology* (17), *Acta Scientiarum. Agronomy* (13), *Acta Scientiarum.Biological Science* (12), *Floresta e Ambiente* (12), *Anais da Academia Brasileira de Ciências* (8), *Hoenhea* (8), *Rodriguésia* (6), *Brazilian Journal of Plant Physiology* (4).