

REVIEW

Pollination in the *campo rupestre*: a test of hypothesis for an ancient tropical mountain vegetation

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The *campo rupestre* is a Neotropical OCBIL (old, climatically buffered infertile landscape), a grassy-shrub vegetation with high species richness and endemism, characterized by rocky outcrops surrounded by grasslands distributed in South American ancient mountaintops. We tested one OCBIL prediction: the prevalence of long-distance pollinators ensuring cross-pollination across the archipelago-like landscapes of the *campo rupestre*. We described the pollination systems and tested whether their frequency differed across vegetation types and elevation, focusing on long-distance systems. We performed non-systematic and systematic surveys of plants and plant-pollinator interactions across the elevation gradient and vegetation types. We also reviewed the literature on *campo rupestre* pollination and applied an accuracy criterion to infer 11 pollination systems. The bee system was split into large bee (long-distance) and small bee (shorter distances) to test the prevalence of long-distance pollination systems. We surveyed 413 pollinator species, mostly bees (220) and flies (69). Among the 636 plant species studied, the bee pollination system was dominant (56%), followed by wind and hummingbird. Wind, small-bee and fly pollination systems increased with elevation, and small-bee and wind pollination systems prevailed in grasslands. Large-bee and hummingbird long-distance pollination systems remained unchanged with elevation and were more frequent in the highly isolated rocky outcrops corroborating the OCBIL theory.

ADDITIONAL KEYWORDS: Espinhaço Range – long distance pollinators – OCBIL – pollination systems – rocky outcrops – rupestrian grassland – Serra do Cipó – The James Effect.

INTRODUCTION

Ancient mountains hold some of the world's highest plant species richness and endemism (Hopper, 2009; Hopper *et al.*, 2016). They also act as living laboratories for field studies, ranging from species evolution and origins of biodiversity to climate change (Körner, 2004; Payne *et al.*, 2017; Silveira *et al.*, 2019). The high diversity in ancient mountains is overall explained by an accumulation of species, coupled to low extinction

rates over long periods of evolution, that followed the orogeneses of those mountains (Hopper, 2009; Vieira *et al.*, 2015; Vasconcelos *et al.*, 2020). The *campo rupestre* is a tropical grassy-shrub vegetation, distributed on the eastern mountaintops and highlands of South America, mainly across the Espinhaço Range (Fernandes, 2016; Silveira *et al.*, 2016). One key feature of the *campo rupestre* is the archipelago-like vegetation system, in which the rocky outcrops are surrounded by sandy, stony and wet grasslands, bordered by cerrado in the south, caatinga dry forest in the north, and tropical forest on the eastern side (Silveira *et al.*, 2016; Morellato

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& Silveira, 2018; Vasconcelos *et al.*, 2020). A feature that may sustain its high diversity and the extensive composition of endemic flora (Vasconcelos *et al.*, 2020).

The high species diversity and endemism of this ancient mountaintop vegetation system has been explained by the OCBIL theory (old, climatically-buffered, infertile landscape) (Hopper, 2009). OCBIL theory suggests that the *campo rupestre* is shaped by its ancient origin and by its infertile soils, both of which act as the main environmental filters buffered by a mild climate (Hopper *et al.*, 2016; Silveira *et al.*, 2016). OCBIL theory has established grounds for testing seven predictions concerning the patterns of species evolution, diversification and functional traits (Hopper, 2009), further explored by Silveira *et al.* (2020) in the context of the Neotropics, including the *campo rupestre*. However, most predictions still need testing and quantitative assessment, especially for Neotropical OCBILs (Hopper *et al.*, 2016; Silveira *et al.*, 2016, 2020; Morellato & Silveira, 2018).

Here, we explore one important prediction of OCBIL theory: the prevalence of long-distance pollinators necessary for assuring cross-pollination across the archipelago-like landscape, and locally restricted plant populations in the context of the *campo rupestre* Neotropical OCBIL (Hopper, 2009). The hypotheses, broadly named as the James Effect, sustains that the selection for heterozygosity in small/isolated populations is mainly through long-distance pollination and genomic coalescence (Hopper, 2009; Hopper *et al.*, 2016; Silveira *et al.*, 2020). The James Effect can be especially relevant because several species in the *campo rupestre* present reduced dispersibility, relying on self- or undetected mechanisms for seed dispersal (L.P.C. Morellato, pers. obs.; Monteiro *et al.*, 2020), which is another prediction from the OCBIL theory (Hopper, 2009). In this scenario, to avoid inbreeding and ensure genetic variability, small-sized populations are expected to select for strategies such as long-distance cross pollination.

We focus our evaluation of OCBIL hypotheses on the presence, relevance and pervasiveness of long-distance pollination, based on the first extensive survey of the biotic and abiotic pollination systems of the *campo rupestre*, an archipelago-like vegetation that dominates the mountaintop of the third largest mountain chain in South America, the Espinhaço Range (Silveira *et al.*, 2016, 2019). Preliminary reports indicate a high proportion of hummingbird pollination in the *campo rupestre*, compared to other tropical vegetations (Carstensen *et al.*, 2014, 2016; Guerra *et al.*, 2016; Silveira *et al.*, 2016). However, those previous assessments were based on locally intensive surveys on rocky outcrops and surrounding grasslands (Carstensen *et al.*, 2014, 2016). A general evaluation for the pollination systems across the *campo rupestre* vegetation complex and along the elevational gradient has never been conducted until now. We performed a

systematic survey of plant-pollination interactions, a non-systematic plant collection, and a systematic quantitative plant sampling across the elevational gradient and vegetation types of Serra do Cipó in the south Espinhaço Mountain Range (Carstensen *et al.*, 2014; Gustafsson, 2017; Mattos *et al.*, 2019). We widened our dataset with a systematic review of the *campo rupestre* pollination literature. To assure the reliability of the 11 pollination systems assigned for each species, we established criteria of accuracy for our inferences of each species' pollination systems, a necessary measure to support our predictions (Fenster *et al.*, 2004).

Therefore, we described, for the first time, the *campo rupestre* main pollinators and plant pollination systems over the elevational gradient and vegetation types according to our accuracy criterions. Considering the OCBIL theory prediction of long-distance pollination, we asked: how the pollination systems differ along the elevational gradient and across vegetation types? Are the long-distance pollination systems evenly distributed through this archipelago-like landscape? Do the long-distance pollination systems prevail on isolated vegetation types? We expected a predominance of bee-pollinated plants among the *campo rupestre* biotic pollination systems (Carstensen *et al.*, 2014, 2016; Guerra *et al.*, 2016) as found in most plant communities (Ollerton *et al.*, 2011). As predicted from OCBIL theory, we expected that most plant species would be pollinated by medium- to long-range movement animals, such as large bees and hummingbirds, due to the barriers imposed by this archipelago-like landscape to gene flow (see Guerra *et al.*, 2016; Carstensen *et al.*, 2018). Accordingly, we expected that plant species from the rocky outcrop vegetation, the most isolated *campo rupestre* vegetation type, would be more dependent on biotic long-distance pollination than the surrounding grassland matrix, dominated by the Poaceae and Cyperaceae and expected to be pollinated mainly by wind (Carstensen *et al.*, 2014; Wolowski & Freitas, 2015). Lastly, we anticipated that elevation would impose a more severe environmental filter to pollination systems than vegetation types. As elevation increases, the frequency of some pollinators such as bees would be reduced, while other pollinators such as flies may be favoured (Arroyo *et al.*, 1982; Wolda, 1987; Perillo *et al.*, 2017; Santos *et al.*, 2020), due to the changes in the assemblage of flowering plants and environmental conditions (Lefebvre *et al.*, 2018; Mattos *et al.*, 2019).

MATERIAL AND METHODS

STUDY AREA

We performed a survey of the plant-pollination studies carried out on the *campo rupestre*, an ecosystem

dominated by grasslands, covering the Brazilian ancient mountaintops (Silveira *et al.*, 2016). Our focus was the Espinhaço Range, the largest inside country mountain chain in Brazil, extending north-south for about 1200 km across the states of Bahia and Minas Gerais, reaching up to 2100 m in elevation (see Morellato & Silveira, 2018; Silveira *et al.*, 2019). Due to its large geographic extent, the Espinhaço Range borders with key vegetation domains or ecoregions in Brazil: the Atlantic Forest, the cerrado, and the dry forest or caatinga, all considered hotspots of species' diversity and endemism (Myers *et al.*, 2000; Streher *et al.*, 2017; Morellato & Silveira, 2018).

Considered a Neotropical OCBIL (Silveira *et al.*, 2016, 2020), the *campo rupestre* is an overall fire-prone vegetation, characterized by an unique, highly diverse flora that evolved on the mountaintops of the ancient Espinhaço Range as an archipelago-like system dominated by grasslands (Morellato & Silveira, 2018; Vasconcelos *et al.*, 2020). These archipelago-like systems occur across the elevational gradient, and the dominant vegetation types, associated with specific soil conditions such as sandy grasslands, stony grasslands, wet grasslands, rocky outcrops and peat bogs, interspaced by cerrado, hilltop forest islands and gallery forests (Alves *et al.*, 2014; Rocha *et al.*, 2016; Coelho *et al.*, 2018; Mattos *et al.*, 2019).

We conducted our sampling in the *campo rupestre* of the Serra do Cipó, south of the Espinhaço Range, south-eastern Brazil. This area has recently been considered as a separate phytogeographic domain denominated as the Southern Espinhaço Province, with the type locality in the Serra do Cipó National Park, which includes three counties: Santana do Riacho, Jaboticatubas and Cardeal Mota (Colli-Silva *et al.*, 2019). Along the Serra do Cipó mountain, up to 900 m a.s.l., the cerrado wood- and shrubland dominates the landscape. There is a transitional zone around 900 to 1100 m a.s.l. with a mixing of cerrado and *campo rupestre* species on sandy and stony grasslands and large rocky outcrops; the *campo rupestre* defines the landscape on elevations above 1100 m a.s.l. (Silveira *et al.*, 2019). The *campo rupestre* floristic composition is dominated by grasses, and also by sedges and herbs from the families Poaceae, Cyperaceae, Xyridaceae, Eriocaulaceae and Velloziaceae, along with small shrubs from the Asteraceae, Melastomataceae, Fabaceae and Rubiaceae (Mattos *et al.*, 2019).

Our plant survey and sampling sites were distributed in the Serra do Cipó National Park and its buffer zone, the Morro da Pedreira protection area (Mattos *et al.*, 2019), hereafter referred to as Serra do Cipó. The local climate is classified as subtropical highland climate (Cwb) by the Köppen (1948) system, with a dry and cold season (winter) from April/May to October and a wet

and warm season (summer) from October/November to April (Alvares *et al.*, 2013; Le Stradic *et al.*, 2018).

PLANTS AND PLANT-POLLINATOR INTERACTIONS

The survey for plant-pollination interactions was based on a three-fold field collection effort led by some of the authors (Supporting Information, Tables S1, S2): (1) a non-systematic plant survey (flora); (2) a systematic sampling of plant-pollinator interactions; and (3) a systematic plant survey across the elevational gradient. The (1) non-systematic plant survey was conducted from 2012 to 2018 along the elevational gradient of Serra do Cipó, covering five sites ranging from 824–1420 m a.s.l. (see Camargo *et al.*, 2019). These five study sites are included in the Long-term Ecological Research—Campo Rupestre of Serra do Cipó program (LTER-CRSC) established in 2011 (Silveira *et al.*, 2019), described by Rocha *et al.* (2016), Camargo *et al.* (2019) and Mattos *et al.* (2019). The plants collected were opportunistically observed for flower visitors, which were considered pollinators when they contacted the flower reproductive parts (Table 1). We took photos of almost all the species to access information on flower colour, shape and size. More than half of the species were also measured for flower colour spectra (Camargo *et al.*, 2019). These floral traits were used to define the pollination system. The vegetation sampling included woody and shrubby cerrado, wet, stony and sandy grasslands, and rocky outcrops (Rocha *et al.*, 2016).

The second collection (2) was a result of the systematic sampling of diurnal plant-pollinator interactions conducted during the years of 2012 and 2016 (Carstensen *et al.*, 2014, 2016; Gustafsson, 2017). The sampling was carried out at seven sites covering an elevational range of 1073–1260 m a.s.l. with similar wind exposition, soil substrate, vegetation structure (dominated by rocky outcrops, sandy or rocky grasslands) and floral species richness (Carstensen *et al.*, 2014). The flower visitors contacting the reproductive parts were considered pollinators (Carstensen *et al.*, 2014, 2016).

The (3) systematic plant survey was conducted at the same five sites of Projeto Ecológico de Longa Duração - Campos Rupestres Serra do Cipó (PELD-CRSC) defined in the (1) non-systematic plant survey, described by Mattos *et al.* (2019). The systematic survey was conducted in 2016, in 36 plots of 1 m² per site, totalling 180 plots. At every site, we established four 270 m long transects in which we set up nine plots, one every 30 m where all plant types, including grasses and sedges, were sampled (Mattos *et al.*, 2019). Transects were independently distributed in each site to guarantee that all the plots were established in similar elevations. Details for each study site, and elevation and plant richness sampled per site are found in Mattos *et al.* (2019). The systematic

Table 1. Criteria of accuracy applied for the inference of the pollination system of plant species. From the most (Category 1) to the less (Category 5) accurate method of inference. For Categories 1 to 3, the determination of the pollination system is based on direct field observations of the target species; for Categories 4–5 the pollination system is inferred based on indirect evidence. *N* = number of species characterized in each category (total = 636 plant species)

Code	Category	Description	<i>N</i>
1	Pollinator proven	Systematic, direct observations in the field of pollen transfer among flowers by floral visitors pollinating the flower. Data may include evaluation of reproductive success, pollen counting/viability, seed production/viability, time and frequency of visits, floral biology and collection of floral visitors.	35
2	Pollinator defined by direct observation	Systematic, direct observation in the field of a flower visitor contacting the stamen/stigma, flower reproductive apparatus, inferred as pollinator. Data may include time and frequency of the visits, and information on floral biology.	203
3	Pollinator defined by opportunistic observation	Pollinator defined by circumstantial, opportunistic field observation of flower visitors contacting the stamen/stigma. Consider eventual qualitative evaluation of visitation frequency and floral biology.	67
4	Pollinator defined from closely-related species	Pollinator defined based on direct observations of closely-related species of the same genus and with similar floral morphology.	181
5	Indirect definition of pollinator	Pollinator system defined based only on floral morphology and floral attributes observed on the field, photos, herbarium vouchers and general literature.	150

plant survey allowed us to perform the quantitative assessment for plant-pollinator interactions and for biotic and abiotic (wind) pollination systems.

The sites surveyed include all *campo rupestre* vegetation types and represent an elevational gradient associated with environmental variables collected by local weather stations (Fernandes, 2016; Silveira *et al.*, 2019). If a plant species sampled in the systematic survey of plant-pollinators interactions (2) or in the systematic survey of plants (3) was new for our local flora, it was added to the previous survey (1) to produce the final plant species list for this study. The plant species surveyed were identified by taxonomists, and compared to local flora, specialized bibliography and herbaria collections. Voucher specimens were deposited in the Herbarium Rioclarense (HRCB) of the São Paulo State University. Some of the plants were identified from vegetative material and it was impossible to properly collect and deposit herbarium vouchers.

LITERATURE REVIEW

To widen the comprehensiveness of our local survey for plant pollination systems and pollinators, we performed an exhaustive, systematic review of published papers and other material (theses, local papers) addressing plant-pollinator interactions on *campo rupestre*. Our search was performed in the databases: ISI Web of Science (<https://clarivate.com/webofsciencelibrary/solutions/web-of-science/>) all databases option,

and Scopus. We also search Google Scholar and BDTD (Biblioteca Digital Brasileira de Teses e Dissertações—Brazilian Digital Database on Thesis and Dissertations) to access unpublished material and “grey” literature. The literature review comprised all the studies available in the cited databases until June 2018. We used the terms: “pollinat*”, “floral biology”, “reproductive biology”, also in Portuguese (polin*, “biologia floral”, biologia reprodutiva”) combined with the terms for the region of interest: “campo rupestre”, “serra do cipo”, “rupestrian”, “montane grassland*”, “altitudinal”, “espinha*o”, “cerrado” and “rupic*”. The search results were further filtered to retain just the research conducted in Brazil and in habitats similar to those sampled here (cerrado, *campo rupestre* and other montane grasslands). Finally, for species on our final plant list with no information for pollinators, we performed a cross-search in the same databases using the species name (e.g. *Palicourea rigida*), regardless of the vegetation type.

LIST OF POLLINATORS

Each flower visitor of the plant species collected during our plant-pollination systematic field survey and in the literature review was annotated, along with the data on visitation frequency, when available. Most of the pollinators in our list were identified based on our field observations (Carstensen *et al.*, 2014, 2016; Gustafsson, 2017). For the literature review, we

noted the visitor as a pollinator based on the author's indication and, if not available, on the description of the animal touching the reproductive parts of the flower, visitation frequency, and whether it was listed as the main pollinator. We organized pollinator species in eight functional groups *sensu* Fenster *et al.* (2004) (Supporting Information, Table S2): bees, wasps, hummingbirds, beetles, butterflies, moths, bats and flies.

We checked species' names looking for synonyms and the most recently accepted name for bees according to Moure's Bee Catalogue (<http://moure.cria.org.br/>), for other pollinator species in the Brazilian Fauna Taxonomic Catalogue (<http://fauna.jbrj.gov.br/>) and for plant species we used Plantminer (Carvalho *et al.*, 2010) and Flora do Brasil 2020 (BFG, 2020).

POLLINATION SYSTEMS

We established 11 pollination systems considering the categories generally used in the studies of plant-pollination systems (Ollerton *et al.*, 2019), our field observations and literature survey: bee, hummingbird, fly, butterfly, moth, bat, wasp, beetle, bee and others, diverse animals and wind (Figs 1, 2). The plant pollination system characterized as "bee and others" considered two functional groups of pollinators of similar relevance for pollination according to the frequency of visitation [e.g. bees and hummingbirds, bees and flies, bees and butterflies; modified from Ollerton *et al.* (2019)]. The category "diverse animals" was assigned when a flower species receives three or more different functional groups of pollinators with same frequency of visitation (Ollerton *et al.*, 2019). Since we have found animals from different taxonomic groups and sizes interacting with one plant species, we considered more appropriate the denomination "diverse animals" pollination system rather than the common designation of "small diverse insects" (Bawa *et al.*, 1985; Gottsberger & Silberbauer-Gottsberger, 2006). Some pollination systems and pollinators were not detected in our study, such as non-flying mammals, ants and saprophytic flies. Ants and hemipterans were frequent visitors; however, our survey did not indicate those insects as main pollinators and they were included in the "diverse animals" pollination system.

To specifically analyse the role of long-distance pollinators along the elevational gradient and vegetation types, we separated bees, within the bee pollination system, into two guilds, only for the plants species from the systematic survey (3). Considering that a bee's body size is positively related to their flight range (Greenleaf *et al.*, 2007), we separated bees into: small bees with body size < 12 mm, considered to pollinate over short distances, and large bees, including medium (12–13 mm) and large (> 13 mm) size bees,

capable to fly over long distances (Frankie *et al.*, 1983; Gottsberger & Silberbauer-Gottsberger, 2006). Bee size was determined based on the author's collection during field work, literature survey and specialized literature (e.g. Urban, 2006; Marchi & Alves-dos-Santos, 2013). For 18 bee species identified at the tribe or subfamily level, size was considered indeterminate and they were disregarded in the analysis. Therefore, according to the frequency of visitation, 'large bee' included plants pollinated mainly by medium to large to bees (long-distance pollinators), and small bee included plants pollinated mainly by small bees (short-distance pollinators), hereafter considered in the analyses as "large bee" pollination system and "small bee" pollination system. Bats and hummingbirds were considered as long-distance pollinators based on their body size and flight distance. Although some territorial hummingbirds do not fly over long distances, whenever resources are scarce, they might fly over larger areas and reduce their territorial behaviour (Justino *et al.*, 2012). A recent study also indicated that plants pollinated by birds show higher paternal diversity compared to plants pollinated solely by insects, as a combination of the behaviour and the high mobility of this functional group (Krauss *et al.*, 2017). However, contradictory results are reported for *campo rupestre* systems pollinated by bees and hummingbirds (e.g. Franceschinelli *et al.*, 2006), a matter worthy of additional investigation. We recognize that other pollination systems may include long-distance pollinators (e.g. moth, butterfly); however, our actual knowledge of the species' natural history and the number of species was not sufficient for a quantitative analysis, thus deserving future research.

We conceived five categories, or levels, of accuracy of the pollination system assigned for each plant species surveyed based on the criteria applied to define the pollinator (Table 1), adapted from Ollerton *et al.* (2019). Categories 1 to 3 include direct observations in the field of flower visitors. Categories 4 and 5 are indirect inferences of the pollination system in which no direct observation was performed by the authors or found in the literature. In Category 4, the pollination system was assigned based on the occurrence of the same pollination system on a closely-related species with similar flower morphology observed in the field. Category 5 included all species with none of the previous information (Categories 1–4), and the inference of pollination system was based on flower morphology observed in the field, photos and in the general literature on pollination (e.g. Faegri & Van der Pijl, 1979; Gottsberger & Silberbauer-Gottsberger, 2006). The accuracy criteria were largely applied for biotic pollination, the focus of most pollination studies on *campo rupestre* (Carstensen *et al.*, 2014, 2016; Guerra *et al.*, 2016). Abiotic pollination by wind

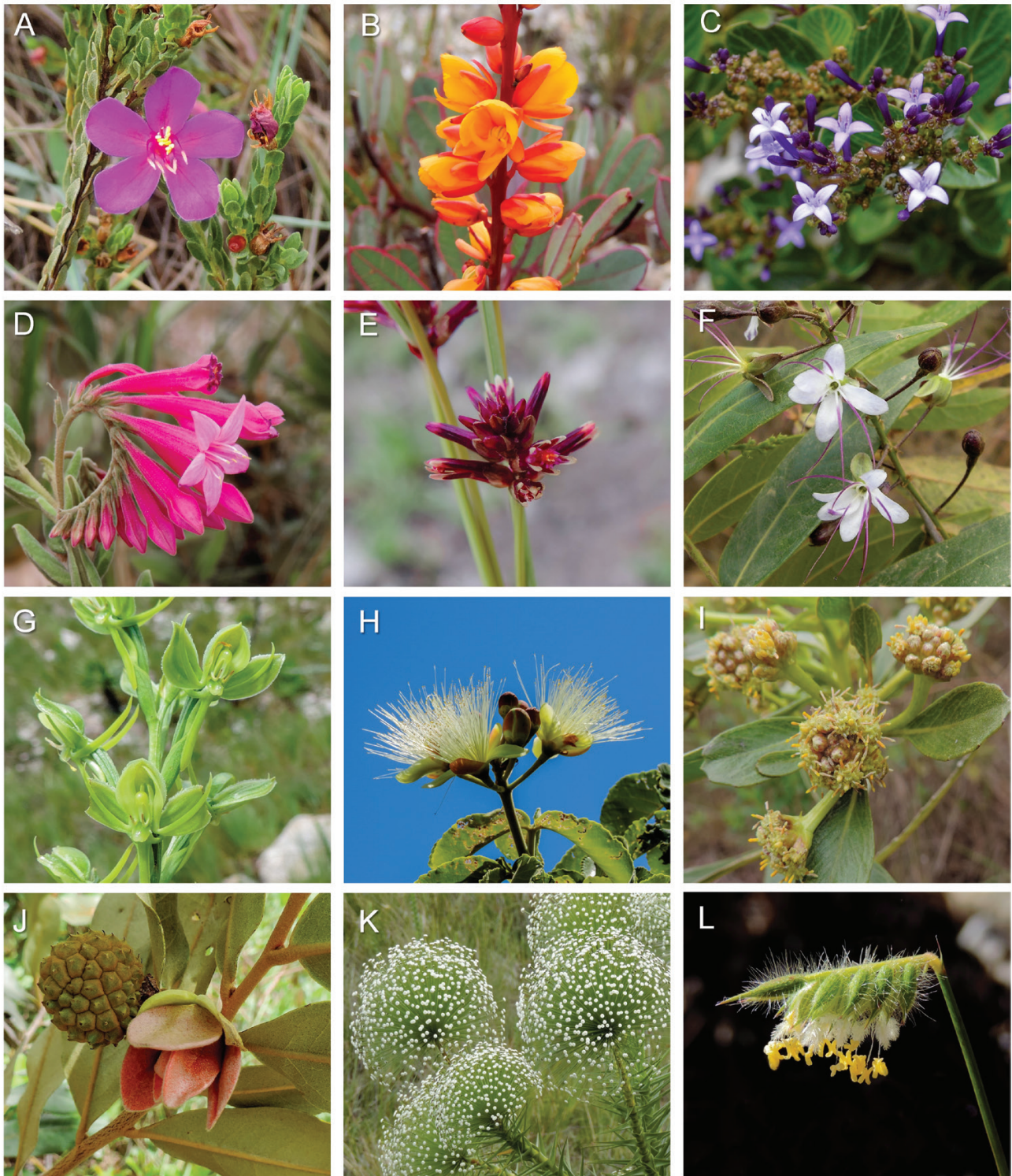


Figure 1. Flowers of plant species from the *campo rupestre* exemplifying the pollination systems adopted in this study. A, bee (small bee pollinated): *Microlicia hirticalyx*. B, bee (medium/large bee pollinated): *Chamaecrista ochracea*. C, bees and others: *Declieuxia fruticosa*. D, hummingbird: *Spigelia sellowiana*. E, fly: *Xerosiphon aphyllus*. F, butterfly: *Hirtella glandulosa*. G, moth: *Habenaria magniscutata*. H, bat: *Caryocar brasiliense*. I, wasp: *Baccharis platypoda*. J, beetle: *Duguetia furfuracea*. K, diverse animals: *Actinocephalus polyanthus*. L, wind: *Echinolaena inflexa*. Photos: M.G.G. Camargo.

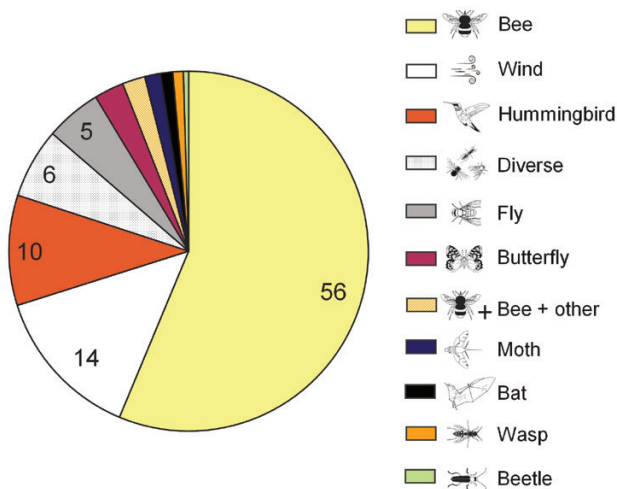


Figure 2. Percentage of *campo rupestre* plant species by pollination system: bee, wind, hummingbird, diverse animals, fly, butterfly, bee and others, moth, bat, wasp and beetle, for the total of 636 plant species. See Supporting Information (Table S1) for details.

predominates among grassland species of the Poales (Wolowski & Freitas, 2015), in which flowers are small and unattractive. Wind pollination has been largely inferred based on flower morphology (Whitehead, 1969; Faegri & Van der Pijl, 1979; Wolowski & Freitas, 2015), a pollination system that fits our Category 5, although we recognize the accuracy is much higher when inferring for this kind of system. Few studies address anemophily, and ambophily has been observed for a limited number of species from groups broadly considered anemophilous (e.g. Oriani *et al.*, 2009; Costa & Machado, 2012; Wolowski & Freitas, 2015; Schulze-Albuquerque *et al.*, 2020). In most cases, we inferred the pollination systems of the plants identified up to species level, to achieve the best accuracy. However, for our analysis based on the plant systematic survey (3), the pollination systems of taxonomically complex groups such as the Poaceae and Cyperaceae, considered mostly anemophilous, were inferred regardless of the species identification level (Supporting Information, Table S1).

DATA ANALYSES

To test whether there was a difference in the pollination systems along the elevational gradient, we used the pollination systems and their respective frequency based on the number of plant species sampled by plot in the systematic survey (3). Each plant species was assigned to one pollination system, given that the bee pollination system was split into two guilds hereafter considered as “large bee” and “small bee” pollination systems. We first applied linear regression models,

with the number of species within each pollination system per plot, that is, the frequency of pollination systems per plot, and the elevation of the plots.

To verify whether vegetation types differed concerning their pollination systems along the elevational gradient, we applied generalized linear mixed effect models [GLMM (Bates *et al.*, 2015)], using elevation and vegetation types as fixed factors. We calculated the plant richness of each plot and used it, together with the transects of the experimental design, as random factors. Then we applied ANOVA tests ($\alpha < 0.05$) to select the best model explaining the variance of our data, following the AIC criteria (Bates *et al.*, 2015). We tested the significance of each explanatory variable using the ANOVA function in the car package (Fox & Weisberg, 2019). We then performed multiple comparisons, based on LMM, to compare the frequency of pollination systems across vegetation types using the emmeans package (Lenth, 2020). All analyses were implemented in R v.4.0.0 (R Development Core Team, 2020).

RESULTS

PLANT SURVEY

We compiled a list of 689 plant species, 555 identified to species level and remaining at morpho-species, from about 1285 samples collected in the plant surveys (1) and (2), plus species included by the systematic plant survey (3) (Supporting Information, Table S1).

LITERATURE REVIEW

The literature survey returned a total of 296 works, from which 82 were retained according to the established search criteria. From the selected studies, 39 were carried out in rupestrian grasslands or *campo rupestre*, 34 were in cerrado and nine studies were conducted in other vegetations. From the 39 studies developed in the *campo rupestre*, 16 were in the Serra do Cipó, 12 in the north of Espinhaço Range (Chapada Diamantina) and the remaining 11 in other localities (Supporting Information, Table S1). From our literature review, we added to our list the pollinators and pollination system for 81 plant species from Serra do Cipó and other *campo rupestre* locations (Supporting Information, Table S1).

LIST OF POLLINATORS

We surveyed a total of 413 species of pollinators belonging to 47 animal families, observed and identified to the species level or morphospecies in the studies conducted by the authors. We included

pollinators identified only to species level from the literature review (Supporting Information, Table S2). The number of species according to the eight broad functional groups of pollinators (Supporting Information, Table S2) showed a prevalence of bees as pollinators and a similar number of both large and small bees (Fig. 3).

Based on our systematic plant-pollinator survey (2), we found 1511 interactions among 413 species of pollinators and 218 species of plants from *campo rupestre*. Bees were responsible for 67.6% of all pollinator interactions, followed by flies and hummingbirds, at 8.8% and 7.1%, respectively. The other five functional groups accounted for the remaining 16.5% of the interactions: wasps (6.0%), beetles (5.8%), butterflies (4.4%), bats (0.2%) and moths (0.07%). The main pollinators were Apidae bees from the subfamilies Apinae, Halictinae and Megachilinae; the Trochilidae hummingbirds; and the Vespidae wasps (Table 2). The main species in number of interactions were the bees: *Apis mellifera*, *Bombus pauloensis* and *Dialictus* sp.1, responsible for 11% of all observed interactions.

POLLINATION SYSTEMS

We determined and quantified the pollination systems for a total of 770 plant species, 689 from our surveys, 555 identified up to species level, plus 81 from the literature review (Supporting Information, Table S1). From the total of 636 fully identified plant species, 48% of the pollination systems were assigned based on direct observations (Category 1 to 3, Table 1); 5.5% of the pollination systems were inferred based on

direct observations in the field of pollen transfer, our most accurate criteria (Category 1, see full description in Table 1), 32% were inferred based on direct observation in the field of a floral visitor contacting flower reproductive parts (Category 2—Table 1) and 10.5% in Category 3 (Table 1). In the remaining 52% of species the pollination systems were defined indirectly: for 28.5% of species, the pollination system was based on direct observations of a congeneric species with similar flowers (Category 4, Table 1), and for 23.6% of species, the pollination system was based on the flower morphology and floral traits (Category 5, Table 1). Wind pollination represented 51.3% of the system species in Category 5.

Our survey showed a dominance of biotic pollination, present in 86.2% of the 636 species evaluated, whereas the remaining 13.8% of species showed abiotic pollination by wind (Fig. 2; Supporting Information, Table S1). Overall, bee was the main pollination system, observed for 56.3% of the plant species, followed by the wind (13.8%) and hummingbird (9.9%) pollination systems (Fig. 2).

Pollination systems across the elevational gradient and campo rupestre vegetational mosaic

We determined the pollination systems of 437 angiosperms sampled in the systematic survey (Fig. 4; Supporting Information, Table S1). The systematic survey showed the predominance of the bee pollination system across the elevational gradient and vegetation types (Fig. 4A, B), representing 45–50% of species, except in wet grasslands (27.8% of species). Considering the frequency of all pollination systems in the *campo rupestre*, wind pollination predominated

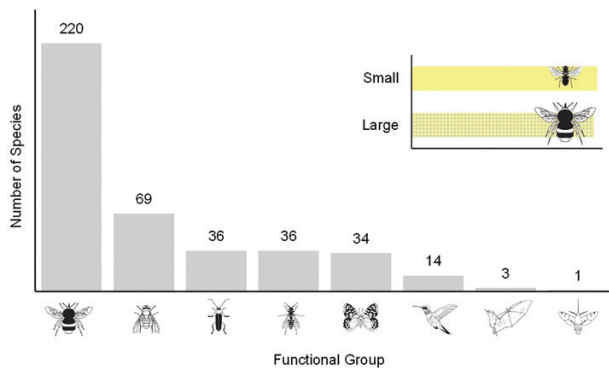


Figure 3. Number of pollinator species ($N = 413$) observed in the systematic sampling of plant-pollinator interactions in the *campo rupestre* of Serra do Cipó according to the taxonomic groups: bees, flies, beetles, wasps, butterflies, birds (hummingbirds), bats and moths. Insert, detail of the number of bee species by size class: small (< 12 mm) and large (medium to large bees > 12 mm). For eight species the bee size was undetermined. See Supporting Information (Table S2) for details.

Table 2. The five broad functional groups of pollinators in the *campo rupestre*, their pollination system, and the number (N) and proportion (%) of plant-pollinator interactions (total of 1511 records). Note four out the five families are Hymenoptera (bee and wasp). For details see Supporting Information (Table S2)

Functional group	Pollination system	Pollinator interaction	
		N	%
Apidae-Apinae	Bee	637	42.2
Apidae-Halictinae	Bee	263	17.4
Trochilidae	Hummingbird	107	7.1
Apidae-Megachilinae	Bee	104	6.9
Vespidae	Wasp	50	3.3
Other families	Other	350	23.2

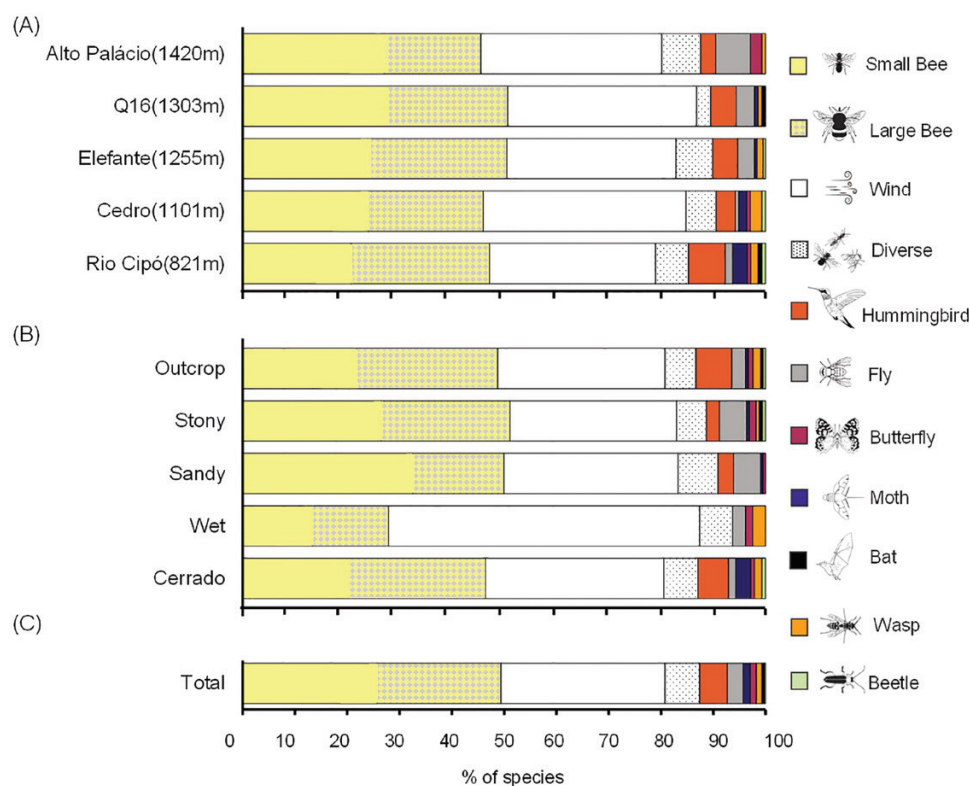


Figure 4. Percentage of plant species sampled in the systematic survey along the elevational gradient of Serra do Cipó, by pollination system: bee, wind, diverse animal, hummingbird, fly, butterfly, moth, bat, wasp and beetle. A, according to the elevation: Alto Palácio ($N = 136$ species), Q16 ($N = 144$), Elefante ($N=186$), Cedro ($N = 137$), Rio Cipó ($N = 142$). B, by vegetation type: rocky outcrop ($N=219$), stony grassland ($N=157$), sandy grassland ($N=198$), wet grassland ($N=79$) and cerrado ($N=138$). C, total of species systematically sampled ($N=437$). Large bees are the hatched area in the yellow bee-pollination system.

in all elevations and vegetation types (Supporting Information; Fig. S1). Along the elevational gradient, the proportion of hummingbird pollination system decreased from 7.0% at the lower elevation to 2.9% in the highest elevation site (Fig. 4A). Conversely, the fly pollination system which is more frequent (6.6%) at higher elevation, decreased to less than 2% at lower elevations. The proportion of bee and wind pollination systems did not change with elevation (Fig. 4A). The wind pollination system dominated the wet grasslands, reaching 59.5% of species, followed by 27.8% of bee pollination (Fig. 4B). There was no hummingbird, bat, moth or beetle pollination system in wet grasslands (Fig. 4B; Supporting Information; Table S1). Indeed, the butterfly, moth, bat, wasp and beetle pollination systems were usually absent or reached values below 1% of species sampled in any vegetation type, except for wasp on wet grasslands and moth pollination in cerrado (Fig. 4B). Diverse animals was generally the third most frequent pollination system, similar to the hummingbird system in cerrado and rocky outcrops.

Linear regression models indicated significant positive relationships between the frequency of wind, fly and small bee pollination systems and elevation (Fig. 5A–C; Table 3). Large bee and moth pollination system frequencies showed significant relationships with elevation; however, with unreliably low predictive power ($\sim R^2 = 0.05$). Therefore, we did not consider these as valid relationships (Fig. 5D and E). The hummingbird pollination system was not significantly related to elevation (Fig. 5F).

Generalized mixed-models revealed significant factors influencing the distribution of the pollination systems along the environmental gradient (i.e. elevation and vegetation types). The ANOVA selection accounted for vegetation types in most cases, whilst elevation was selected in only one case, explaining the distribution of the fly pollination system (Table 4). Transects were selected in the hummingbird model, and plant richness was selected in all other pollination systems (Table 4). The wind pollination system was positively related to elevation ($R^2 = 0.25$, Table 3), and

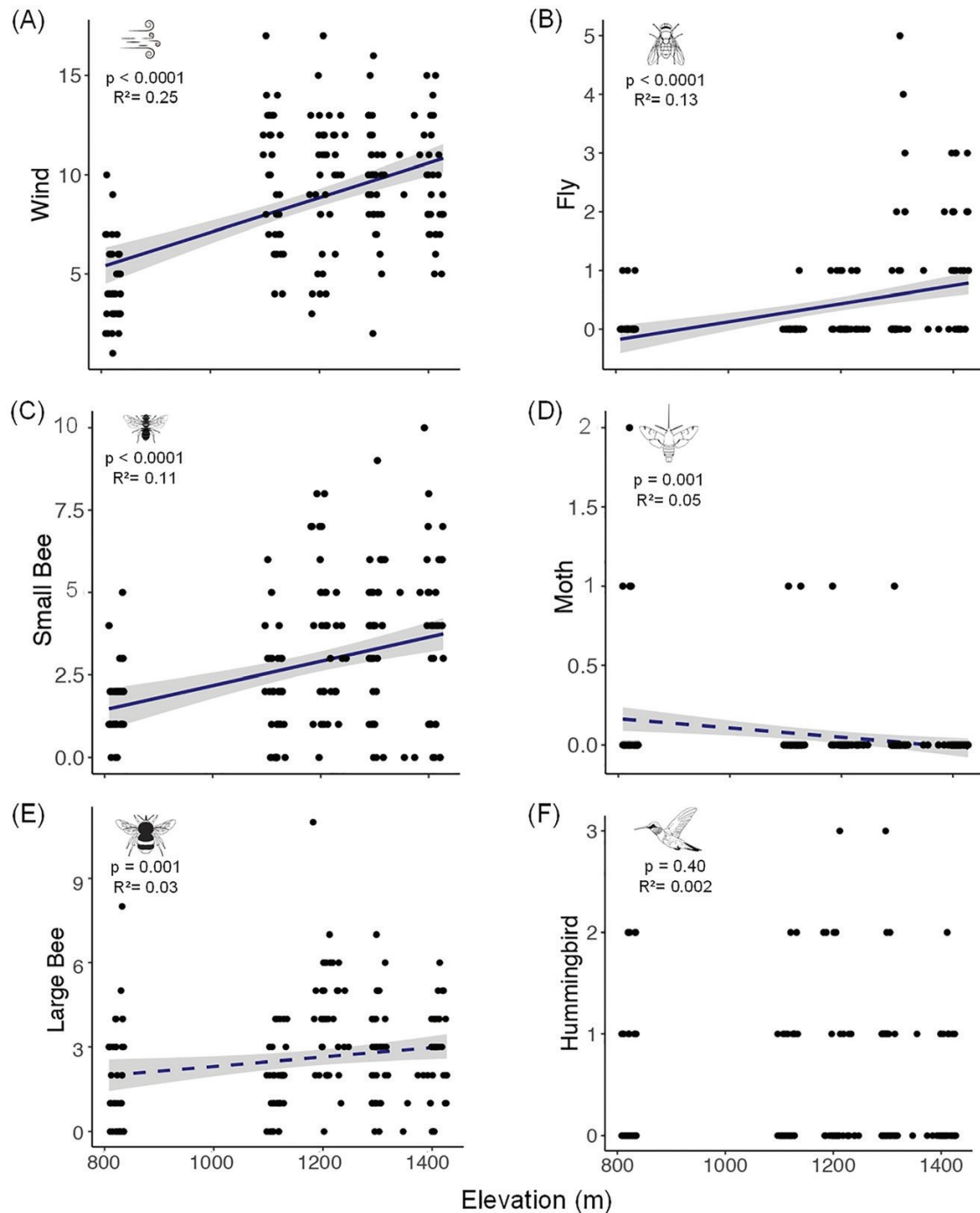


Figure 5. Linear regression between the frequency of pollination systems in 180 plots along the elevational gradient in the *campo rupestre*. The relationship significance (p) and predictive power (R^2) are indicated in each graph. A, wind. B, fly. C, small bee. D, moth. E, large bee, F, hummingbird.

this relationship was significant in the mixed-models; however, the lower AIC model included vegetation type (Pseudo- $R^2 = 0.56$, Table 4) and not elevation. The differences among vegetation types through mixed-models indicated that sandy and stony grasslands

presented a higher frequency of wind and small bee pollination systems (Fig. 6A, B). The frequency of species with the diverse animal pollination system was high in the cerrado and remarkably low in stony grasslands (Fig. 6F). The mixed-models for the fly

pollination system selected elevation, accounting for species richness, increasing the explanation of the simple linear model to 30% (Table 4).

The generalized mixed-models selected for both large and small bee pollination systems included vegetation types and plant richness (Table 4). Variation on the small bee pollination system was supported by the full-model (Pseudo- $R^2 = 0.74$, Table 4) and this pollination system occurred more often in sandy and stony grasslands (Fig. 6B). The large bee pollination system was slightly positively related to elevation, and differed among some vegetation types when accounting for plant richness ($P < 0.001$, Conditional $R^2 = 0.29$), being more frequent in rocky outcrops and stony grasslands (Fig. 6C). The distribution of hummingbird and wasp (Fig. 6D, E) pollination systems were not related to elevation and less explained by any of the models (mixed-models were the best, explaining 20 and 11%, respectively), with an outstanding role of

rocky outcrops, hosting most of these long-distance pollination systems (Fig. 6C, D).

DISCUSSION

Our study provided the first systematic, broad description of pollinators and pollination systems for the *campo rupestre*, a Neotropical OCBIL. Our data and analysis supported the OCBILs theory prediction of high occurrence of long-distance pollinators and its prevalence in an isolated vegetation type. We demonstrated (1) the overall occurrence of long-distance pollination systems (mainly large bee and hummingbird) along the *campo rupestre* elevational gradient and vegetation types; and (2) their prevalence on isolated rocky outcrops, essential for cross-pollination across this archipelago-like landscape. We also demonstrated the expected dominance of bee and wind pollination systems in the *campo rupestre* grassy landscape. Furthermore, for the first time, we revealed the increase of the fly pollination system with elevation for this old, low, snow-free mountain vegetation, along with small bee and wind systems, trends that will be discussed in the sections below.

POLLINATORS AND POLLINATION SYSTEMS IN CAMPO RUPESTRE

The high diversity of pollinators and pollination systems disclosed here were expected for tropical vegetation and mountain systems [see Table 5 for references; Ollerton *et al.* (2011); Queiroz *et al.* (2019)]. After the Apidae, hummingbirds of the Trochilidae, mediated a large number of interactions (7.1% of 1511 interactions), confirming the relevance of bees and hummingbirds for free-living mutualistic interactions in the *campo rupestre* (Carstensen *et al.*, 2014, 2016; Guerra *et al.*, 2016).

Table 3. Results of linear regression models for each pollinator system and the elevation of the plots

Pollination system	P value	R ²	Coef1	Coef2
Bee	< 0.0001	0.13	-0.96	0.005
Small bee	< 0.0001	0.11	-2.48	0.004
Large bee	0.001	0.03	0.66	0.001
Wind	< 0.0001	0.25	-1.63	0.008
Hummingbird	0.40	0.002		
Diverse	0.97	0.001		
Fly	< 0.0001	0.13	-1.48	0.001
Butterfly	0.50	0.002		
Bee + other	0.92	7E-04		
Moth	0.001	0.05		-2.93
Bat	0.45	0.003		
Wasp	0.28	0.06		
Beetle	0.48	0.002		

Table 4. Results of generalized linear mixed models (GLMM), after ANOVA selection, for each pollination system, showing fixed and random factors selected in the best model for each pollination system. The P value shown refers to the ANOVA results over models; conditional Pseudo- R^2 shows a measure of power of the entire model (Nakagawa & Schielzeth, 2013). Vegtype = vegetation type (wet, stony, and sandy grasslands, rocky outcrops and cerrado)

Pollination system	Fixed	Random	P value	Pseudo-R ²
Bee	Vegtype	Richness	< 0.001	0.87
Small bee	Vegtype	Richness	< 0.001	0.74
Large bee	Vegtype	Richness	< 0.001	0.29
Wind	Vegtype	Richness	< 0.001	0.56
Hummingbird	Vegtype	Transect	< 0.001	0.20
Diverse	Vegtype	Richness	< 0.001	0.46
Fly	Elevation + vegtype	Richness	< 0.001	0.30
Wasp	Vegtype	Richness	< 0.001	0.11

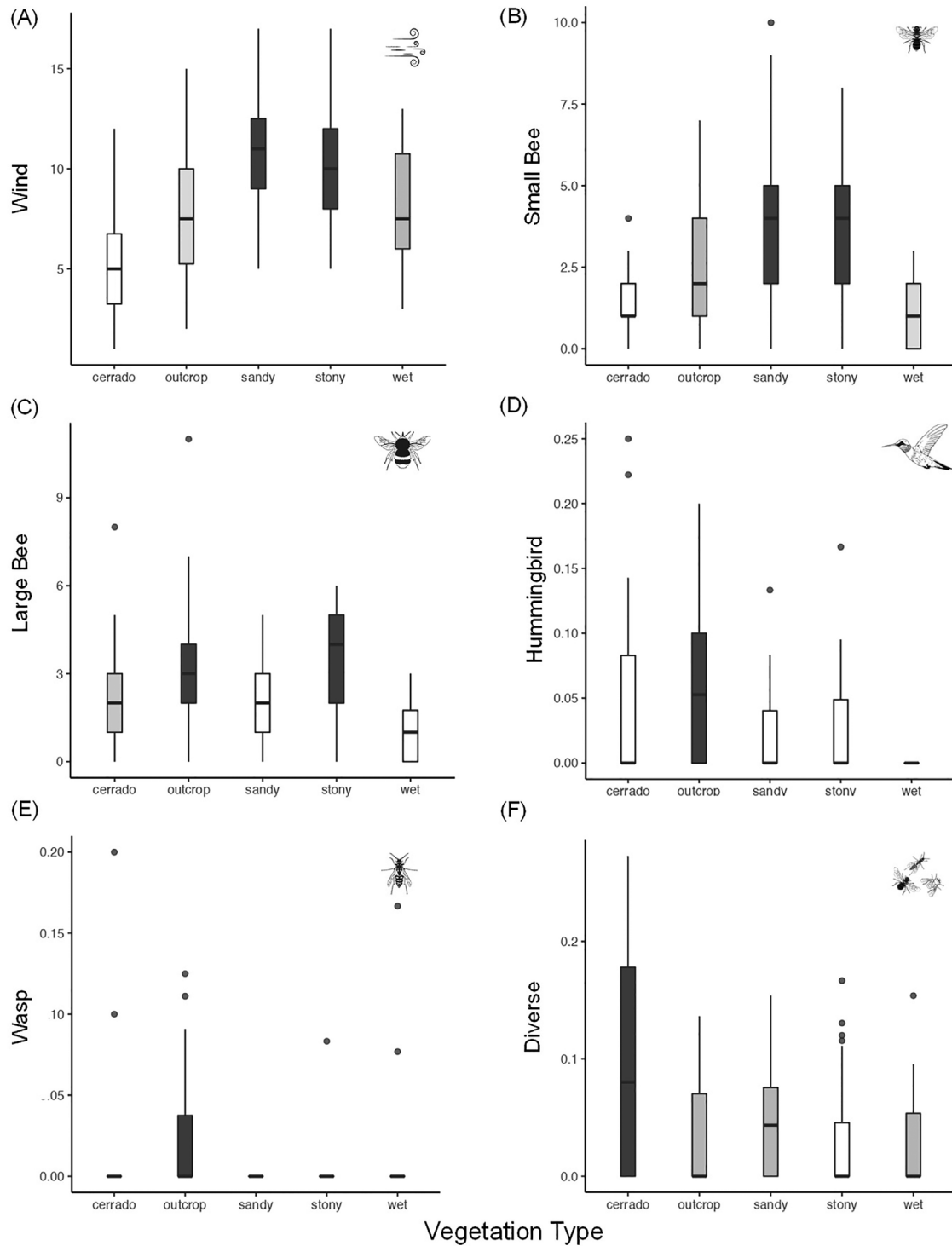


Figure 6. Frequency of pollination systems in 180 plots of *campo rupestre* according to the vegetation types: cerrado, rocky outcrop, sandy grassland, stony grassland and wet grassland. The grey intensity of each box indicates a significant relationship and the white boxes indicate non-significant relationships according to the generalized linear mixed-models. A, wind. B, small bee. C, large bee. D, hummingbird. E, wasp. F, diverse.

Table 5. Comparison of the percentage of pollination systems among diverse vegetations. The green shading indicates OCBILs (old, climatically buffered, infertile landscapes) and the light grey YODFELs (young, often disturbed, fertile landscapes) following [Hopper \(2009\)](#) and [Silveira *et al.* \(2020\)](#)

Vegetation	Study site	Country	Bee (total)	Bird	Fly	Butterfly	Moth	Bat	Beetle	Wasp	Wind	Diverse	Thrip	Reference
Altitudinal grassland	Serra da Bocaina, SP/RJ	Brazil	43.3	4.7	12.3	-	-	-	-	20.8	-	18.9	-	Freitas & Sazima (2006)
<i>Campo rupestre</i>	Mãe Inácia Peak, Palmeiras, BA	Brazil	63*	29.0	-	-	-	2.0	-	-	6.0	-	-	Conceição <i>et al.</i> (2007) §
<i>Campo rupestre</i>	Serra do Cipó, MG	Brazil	56.3	9.9	5.0	2.7	1.4	1.1	0.5	0.9	13.8	6.3	-	This study
<i>Campo rupestre</i>	Serra do Cipó, MG	Brazil	48.3	5.3	3.0	1.1	1.4	0.5	0.2	1.1	31.4	6.6	-	This study (systematic)
Canga	Iron Quadrangle, MG Brazil	Brazil	77.0*	13.0	-	-	-	-	-	-	16.0	-	-	Jacobi & Carmo (2011) §
Cape floristic region (Fynbos)	Jonaskop Mountain	South Africa	53.5	-	8.9	-	-	-	28.5	9.1	-	-	-	Adedjoja <i>et al.</i> (2018)
Altitudinal scrubland	Parque Nacional Canaima	Venezuela	56.2	12.3	9.6	10.9**	-	-	2.7	-	8.2	-	-	Ramirez <i>et al.</i> (1990)
Andean	Higher altitude	Argentina	28.6	0.0	4.8	0.0	-	0.0	4.8	4.8	-	0.0	4.8	Medan <i>et al.</i> (2002)
Andean	Lower altitude	Argentina	39.1	8.7	8.7	8.7	-	0.0	0.0	0.0	-	0.0	0.0	Medan <i>et al.</i> (2002)
Andean	Andes	Chile	11.4	0.0	25.7	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0	Arroyo <i>et al.</i> (1982)
Cerrado	Brasilia Botanic Garden, DF	Brazil	32*	2.0	-	0.0	12.0	3.0	2.0	-	0.0	44.0	0.0	Oliveira & Gibbs (2000)
Cerrado	Fazenda Treze de Maio, Botucatu-SP	Brazil	37.9	1.7	1.3	1.0	4.3	1.0	2.7	-	13.3	36.9	-	Gottsberger & Silberbauer-Gottsberger (2006)
Cerrado	Triangulo mineiro, MG Brazil	Brazil	83.2	3.4	2.3	2.3	3.4	3.9	1.7	-	-	-	-	Silva <i>et al.</i> (2012)

*Entomophily.

**Includes moths.

§Pollination syndromes.

As a functional group, flies responded for a high amount of the plant-pollinator interactions (8.8% of 1511), a result anticipated for mountain systems (Lefebvre *et al.*, 2018), but only corresponded to 5% of the total plant pollination systems (Table 5). Freitas & Sazima (2006) described the fly pollination system for 12% of the plants from altitudinal grasslands, another Brazilian OCBIL system (Silveira *et al.*, 2020). Although important in these OCBIL environments, fly pollination is even more important in YODFELs (young, often disturbed, fertile landscapes) mountain systems, accounting for up to 25% of the pollination systems in such areas (Arroyo *et al.*, 1982). It is worth noting that fly pollination is a particularly important, highly specialized pollination system in South African fynbos, relevant for plant species diversification in that OCBIL vegetation (Johnson, 2010). However, the extreme specialization of southern African pollination guilds is unmatched, and more natural history observation is needed to uncover the role of “pollination system niche” (Johnson, 2010; Phillips *et al.*, 2020) on the evolution and diversification of the *campo rupestre*.

We confirmed the expected prevalence of bee pollination for the *campo rupestre*, followed by wind and hummingbird pollination systems. Our findings differed from a survey for another *campo rupestre* area at North Espinhaço (Chapada Diamantina Province, *sensu* Colli-Silva *et al.*, 2019) where anemophily accounted for 6% of the plant pollination, and hummingbird pollination for about 30% (Conceição *et al.*, 2007). However, a study conducted at the canga, an ironstone rocky grassland in southern Espinhaço Province, has reported 13% of hummingbird pollination (Jacobi & Carmo, 2011) and only 5% has been registered for altitudinal grasslands (Freitas & Sazima, 2006).

In contrast with the well-defined pollination systems, the diverse animal pollination system had a low contribution when compared to the cerrado (Table 5). However, it is hard to compare vegetations, since this pollination system has different definitions according to the study methodologies and goals (Table 5). In our survey the Eriocaulaceae, one of the most abundant families in the *campo rupestre* (Mattos *et al.*, 2019), was the best represented family within the diverse animal pollination system although some detailed studies have shown otherwise (e.g. Ramos *et al.*, 2005; Del Claro *et al.*, 2019). The minor contribution of bat and moth pollination systems might be partially explained by the focus on day light observations, however, these systems are not representative of the *campo rupestre*.

POLLINATION SYSTEMS ACROSS THE CAMPO RUPESTRE VEGETATIONS AND ELEVATIONAL GRADIENT: TESTING THE OCBIL HYPOTHESIS

Our study provided evidence for the predominance of pollination systems related to long-range pollinators, necessary for ensuring cross-pollination in the archipelago-like landscape, and locally restricted plant populations of the *campo rupestre*, as proposed by the OCBIL theory. Firstly, we demonstrated, based on systematic plant survey, that the frequency of long-distance pollination systems, such as large bee and hummingbird, were not affected by elevation. The occurrence of both long-distance pollination systems across elevations supported the OCBIL hypotheses, assuming that the constancy of long-range pollinators likely assures outcrossing and wider pollen flow (Hopper, 2009; Silveira *et al.*, 2020). Hummingbirds and large bees are known to occur along the elevational gradient of Serra do Cipó. Rodrigues *et al.* (2011) indicate the Trochilidae is the species-rich families of hummingbirds on high elevations of Serra do Cipó grasslands. A similar pattern has been described for some groups of medium and large bees (Perillo *et al.*, 2017; Santos *et al.*, 2020). Secondly, long-distance pollination systems such as hummingbird and large bee were associated with rocky outcrops, the most isolated vegetation type in the *campo rupestre*, while small bee and wind prevailed across the grasslands, and diverse animal in the cerrado. Therefore, our findings corroborated the OCBIL long-distance pollination hypothesis, indicating its prevalence in isolated vegetation of rocky outcrops. Hummingbirds represent one of the most diverse bird families on rocky outcrops and are highly dependent on the floral resources present in this vegetation type (Rodrigues *et al.*, 2011; Rodrigues & Rodrigues, 2014), although they can use alternative food sources such as insects. The higher proportion of species pollinated by hummingbirds in the *campo rupestre* and other OCBILs, when compared to YODFEL and other cerrado, added support for the prevalence of long-distance pollination (Table 5 and references therein).

Our evidence that in a low, old, snow free mountain system, elevation indeed affected the frequency of species within some pollination systems is of utmost importance. To our knowledge, there is no available community-level study specifically addressing the influence of elevation gradients and landscape heterogeneity on the patterns of distributions of plant pollination systems on the *campo rupestre* (see Table 5). Our analysis demonstrated that bee and wind are the main pollination systems along the elevational gradient. There was a significant increase in the frequency of wind, small bee and fly pollination

systems with elevation, here described for the first time for a tropical snow-free mountain vegetation. The increase of fly pollination is especially relevant, since some Syrphidae flies may act as medium distance pollinators (Rader *et al.*, 2011). Increasing fly pollination with elevation has long been described for the young, high mountain systems (Wolda, 1987; Lefebvre *et al.*, 2018) and some Neotropical YODFELs (see Table 5), with a change in importance from bee to fly pollination (Arroyo *et al.*, 1982; Medan *et al.*, 2002; Lefebvre *et al.*, 2018). In fact, Syrphidae and Tachinidae species represented 20% and 13% of the observed flies, respectively, in our survey and were responsible for 36% and 18% of the registered fly interactions in our *campo rupestre*.

Regarding bee pollination, overall abundance and richness of bee species decrease with elevation in *campo rupestre* vegetation (Perillo *et al.*, 2017; Santos *et al.*, 2020). However, we argue that there is no strong environmental restriction related to the elevational gradient for large bee movement in these old tropical mountains. Therefore, they could act as important pollen vectors all over the landscape, alongside flies at higher elevations.

Finally, around 94% of plants from tropical communities are expected to rely on biotic vectors for pollination (Ollerton *et al.*, 2011). In the *campo rupestre*, 86% of the species presented biotic pollination, but when considering the systematic plant survey, the proportion dropped to 68%. Wind represented the most important pollination system when accounting for species' frequency in the plant systematic survey, reaching around 50% to up 70% of the plant species (Supporting Information, Fig. S1). The wind pollination system was prevalent in all grasslands dominated by anemophilous grasses and sedges (Wolowski & Freitas, 2015; Schulze-Albuquerque *et al.*, 2020), and was exceptionally dominant in wet grasslands, a vegetation type lacking rosette herbs, shrubs and treelets (Mattos *et al.*, 2019). Moreover, recent studies revealed ambophily and insect pollination in plants from groups assumed as anemophilous (Costa & Machado, 2012; Wolowski & Freitas, 2015; Schulze-Albuquerque *et al.*, 2020 and see Friedman & Barrett, 2009). Conversely, the reduced occurrence of grasses and sedges in the rocky outcrops and cerrado (Mattos *et al.*, 2019) explained the decline of wind pollination in those vegetation types. Therefore, resources for pollinators seem nested in the outcrops, otherwise sparsely distributed over the dominant grassland matrix, stressing the relevance of long-range pollination systems for cross-pollination and gene flow among isolated endemic plant populations (but see Franceschinelli *et al.*, 2006).

CONCLUSION

Our findings revealed, for the first time, the pollination systems and main groups of pollinators across the *campo rupestre*, confirming the importance of bees and hummingbirds and the high frequency of wind pollinated species. We demonstrated the increased importance of fly pollination at high elevations, a pattern new for Neotropical ancient mountains, along with an increase in the small bee pollination system.

We corroborate the OCBIL long-distance pollination hypothesis, by demonstrating the prevalence of pollination systems associated with large bees and hummingbirds on isolated rocky outcrops, likely promoting outcrosses among plant populations, as well as its persistence across the elevational gradient. The comparison of pollination systems among OCBILs, YODFELs and cerrado, although offering support for the prevalence of long-range pollination systems represented mainly by birds (Table 5), needs in-depth analysis. Methods vary, from the sampling design to the definition and determination of pollination systems all affecting the final proportions. We argue that differences might be more significant among vegetation systems if one can account for all those biases.

The dependence on pollinators that fly over long distances could be among the strategies adopted by the endemic species to endure and escape genetic erosion across the *campo rupestre* (Vasconcelos *et al.*, 2020). Indeed, overall genetic studies are still limited, as seen in the review by Silveira *et al.* (2020). Furthermore, just a few studies address the specific cases of species isolated on rocky outcrops, gene flow and reproductive systems (e.g. Borba *et al.*, 2001; Franceschinelli *et al.*, 2006; Bonatelli *et al.*, 2014; Hmeljevski *et al.*, 2017). Recent genetic evidence indicates that gene flow via seeds is comparatively less efficient than gene exchange via pollen across the Espinhaço Range (Dantas-Queiroz *et al.*, 2020). Further studies on microevolutionary processes should estimate pollen dispersal distance, degree of heterozygosity and overall gene flow across the landscape.

The present extensive database on plant-pollinator interactions holds key information for the conservation and knowledge of ecosystem services of the *campo rupestre*. Likewise, it also opens a huge opportunity for the study of pollination in grasses and sedges, adding to the debate of questions on evolution, restoration and management of grasslands. Our unprecedented study on pollination systems of the *campo rupestre* indicated the relevance of plant-animal interactions that is possibly shaping the diversity of this unique archipelago-like landscape. We advocated that the pollination niche may act as an important selective force, along with the

unfertile soils, driving the evolution and diversification of *campo rupestre* vegetation, as proposed by Johnson (2010) for southern African OCBIL vegetation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Number of species of each pollination system (small bee, large bee, wind, diverse animals, hummingbird, fly, butterfly, moth, bat, wasp and beetle) per plot, or frequency of species, in the systematic survey at the *campo rupestre* of Serra do Cipó.

Table S1. List of species, organized by family, and respective pollination systems, and information on voucher number, survey type, source, category of the accuracy criteria, bee size system, vegetation and study site. For more details, see *Material and Methods*.

Table S2. List of pollinators observed in the *campo rupestre*, organized by family and species, their functional group and bee size category.