

Sexual and Breeding Systems in a Xerophytic Shrubland

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Abstract

Reproductive systems are fundamental attributes for understanding life cycle and regeneration processes and provide information about seed production and genetic diversity. Analyses of reproductive strategies within communities and their associations with functional groups can indicate how physical and biological characteristics may influence the reproductive ecology of such communities. The main goal was to determine if the reproductive systems and their associated functional groups have particular characteristics related to extreme conditions and disturbance within xerophytic shrubland. Floral morphology analysis and four experimental tests were conducted to determine the reproductive systems of species and their associations with the life form, succulence, carbon metabolism, dispersal syndrome, pollination, and disturbance. Of the 144 plant species studied, 72.9% were hermaphrodite, 22.9% were monoecious, and 4.2% were dioecious. Dioecy was associated with woodiness, frugivory and undisturbed areas, while monoecy was more common in herbs. Adichogamy, protandry and herkogamy were more frequent than dichogamy, protogyny and no herkogamy, respectively. Xenogamous species tend to be woody and grow in undisturbed areas, while partially xenogamous species were mainly herbs occurring in disturbed areas. The majority of species were partially self-incompatible. High levels of outbreeding strategies tended to occur mainly in woody K-strategy species from undisturbed areas, mixed breeding strategies occurred in disturbed areas and overall community, and inbreeding strategies were associated with mostly herbaceous r-strategy primarily in disturbed areas.

Keywords

Dichogamy, Dispersal Syndrome, Disturbed Habitat, Herkogamy, Life Form, Pollination System Specificity, Reproductive System

1. Introduction

Drylands comprise large areas of terrestrial ecosystems [1]. In Venezuela, xerophytic areas are located mainly in the northern part of the country and are commonly associated with coastal zones. These stressful areas are characterized by high temperatures, low precipitation and low availability of soil nutrients. Under this regime, plant species exhibit many xeromorphic modifications and adaptations related to their life cycle, such as slow growth and regeneration [2]. In addition, many xerophytic areas are frequently exposed to episodic disturbance driven by torrential rainfall. This together with steep topography produces soil erosion and discontinuous vegetation cover [3], where colonizing pioneer species is very common. However, specific xeromorphic adaptations and reproductive trait associations have not been investigated in detail.

Plant reproductive systems are fundamental attributes for understanding life cycle and regeneration processes and provide information about seed production and genetic diversity. Analyses of reproductive systems within communities and associations with functional groups can indicate how ecological properties may influence the reproductive ecology and evolution of such communities. Functional groups have an implicit relationship with reproductive and demographic processes and in this context are defined as any trait at the individual level that is directly related to reproductive performance or fitness measured by fertility and survival, among other fitness parameters [4]. In addition, the relationship between reproductive systems and regeneration processes allows us to understand how communities persist over time as a whole. The diversity of reproductive strategies associated with different functional groups shows multiple combinations in disturbed and undisturbed environments of the communities [5] [6] [7], which is an approximation to explain the characteristics of the plants in the communities, functional diversity and biodiversity.

Flowering plants exhibit remarkable diversity in their reproductive system, which reflects their adaptation to biotic and abiotic environments. Studying reproductive systems and their correlates at a community scale is very important to an understanding of how environmental factors drive the evolution of the sexual organization and breeding systems. Previous studies have found that abiotic factors contribute to the evolution of dioecy [8] [9] [10]. However, other studies suggest hermaphrodites are likely to occur in stressful environments where selfing can provide reproductive assurance [11] [12] [13] [14] [15]. How reproductive diversity varies with climate, especially with water availability, remains controversial. Two contrasting and extreme plant reproductive strategies have been described: outbreeding and inbreeding. In nature, however, there is a continuum from outbreeding to inbreeding strategies, where various possible combinations of sexual systems, dichogamy, herkogamy and breeding systems, exist [5] [6] [9] [16]. Despite the great diversity of mechanisms promoting outbreeding (see **Table 1** for the definition of reproductive terms), including unisexuality, dichogamy, herkogamy, and self-incompatibility, a substantial number

Table 1. Glossary of reproductive terms used. The definitions agree with those proposed by Cardoso *et al.* (2018), but differ in the organization of the groups.

| Term | Definition |
|--|--|
| Reproductive systems | General term related to the processes of sexual reproduction, form of sexual organization, relationships between gametes, self-incompatibility (breeding systems or genetic reproductive systems) and various forms of asexual reproduction including agamospermy. |
| 1. Sexual organization | The distribution of sexual organs in flowers, individual plants, populations, and species as well as their spatial separation and relative timing in the maturation of sexual organs in flowers, inflorescences or individual plants. |
| 1.1. Sexual systems | Gender expression and its occurrence at different levels: intrafloral, individual, population and species. |
| 1.1.1. Hermaphrodite | Individuals of a population present only bisexual flowers. |
| 1.1.2. Monoecy | Individual of population present unisexual flowers (pistillate and staminate flowers) in the same individual. See methods and Cardoso <i>et al.</i> (2018 for more details). |
| 1.1.3. Dioecy | Unisexual flowers, staminate and pistillate flowers are arranged in different plant of a population. Subdioecy were considered as dioecy. See methods and Cardoso <i>et al.</i> (2018) for more details. |
| 1.2. Herkogamy | Spatial separation anther-stigma within in the same hermaphrodite flower or unisexual flowers of monoecious species. |
| | Non-herkogamy: Herkogamy absence. |
| 1.3. Dichogamy | Temporal separation of sexual functions by the sequential ripening of the androecium or gynoecium in hermaphrodite flower, or by different times of anthesis of staminate and pistillate flowers of monoecious species. Adichogamy: The absence of dichogamy. |
| 1.3.1. Protogyny | Female expression occur previous male. |
| 1.3.2. Protandry | Male expression occur previous female. |
| 2. Breeding systems | Reproductive genetic systems. Reproductive attributes determined by genetic processes. |
| 2.1. Agamospermy | Seed formation asexually. |
| | Seed formation spontaneously by self-pollination. |
| 2.2. Spontaneous self-pollination | It includes four levels according to the levels of spontaneous self-pollination: Non-spontaneous self-pollination. Partially spontaneous self-pollination. Spontaneous self-pollination. Obligated spontaneous self-pollinated. |

Continued

| | |
|---|--|
| <p>2.3. Self-fertility</p> | <p>Expression of cross-pollination capacity. It includes several levels that partially agree with the categories of mating systems described by Cardoso <i>et al.</i> (2018). Partial xenogamy, partial outbreeding Xenogamy, obligate and complete outbreeding. Autogamy, full self-pollination ability. Partial endogamy, levels of selfing higher than levels of outcrossing; very low outcrossing rate.</p> |
| <p>2.4. Self-incompatibility</p> | <p>A genetic based inability of plants to produce fertile seeds aftergoing self-pollination. Four categories were found in this study. Self-incompatibility, inability to produce fertile seeds after self-pollination. Partial self-incompatibility, partial production of seeds by self-fertilization. Self-compatibility, full production of seeds by self-pollination. Partial cross-incompatibility, partial inability to produce seeds by cross-pollination.</p> |

of plant species exhibit different levels of self-fertility, autogamy, self-compatibility and agamospermy at the community level [5] [6] [7] [17].

The frequency distribution of different breeding systems at the community level depends on multiple factors, including taxonomic composition, vegetation structure and geographic insularity [5] [6] [7] [18] [19] [20]. Regarding the association between plant species and functional groups, the plant life form is an important trait associated with plant breeding systems [5] [6] [7] [19] [21], and together with seed dispersal syndromes, pollination systems, and successional stages [5] [6] [7] [20] [22]. The composition of species changes with the regeneration stage of the environment and consequently the most frequent reproductive characteristics. Self-compatibility prevails in early successional stages, while outcrossing occurs more often in later stages as dicliny, dioecism, and self-incompatibility become more frequent [22] [23] [24]. Studies on sexual organization and breeding systems have revealed a predominance of self-compatibility and very low frequency of dioecy in two contrasting dry lands around the world: Galapagos Islands [11] and Paraguaná coastal plain [12]. However, records of selected plants from the Venezuelan Central Coastal xerophytic shrublands have shown the occurrence of self-incompatibility in arborescent and distylous species and self-compatibility only in herbaceous taxa [25] [26] [27].

In addition to associations between reproductive genetic systems and functional groups mentioned above, the breeding system of a species is also critically important both genetically and ecologically for plant conservation strategies. Breeding systems, pollination, and dispersal syndromes are key elements for understanding restoration processes in tropical plant communities [24]. Lack of knowledge about breeding systems in plant species has hindered our under-

standing of species' recovery. Understanding different reproductive strategies allow us to have knowledge of the susceptibility of plant species to collapse under perturbation scenarios. Xerophytic environments may be particularly vulnerable to perturbation, presenting challenges to conservation [1]. Low growth and recruitment of plant species under water-limited conditions represent the main obstacle [2]. Plant species regeneration depends on reproductive efficiency and, consequently, on plant reproductive systems. In fact, fruit and seed set depend to a large extent on plant breeding systems, with self-pollinating species being more efficient than xenogamous, cross-pollinated species [21] [28] [29] [30]. Consistent with reproductive system characteristics, plant reproductive strategies in xerophytic areas represent diverse alternatives for plant regeneration. Xeromorphic adaptations of plant species growing in drylands could be related to specific reproductive traits.

The primary goal of sexual traits analyses has been to assess the relative importance of various selective pressures and understand how they interact in different situations [31]. The present study evaluates the community spectrum and diversity of reproductive systems (sexual organization and breeding systems) in xerophytic shrubland, including disturbed areas. It evaluates if stressful conditions inherent to xerophytic lands are associated with specific reproductive strategies. Additionally, an evaluation is made of whether sexual systems, dichogamy, herkogamy, and breeding systems are associated with functional groups (life form, succulence, carbon metabolism, dispersal syndrome, and pollination system specificity) and how such associations might influence the incidence of reproductive mechanisms promoting outcrossing or inbreeding in undisturbed and disturbed areas of the plant community.

2. Materials and Methods

2.1. Study Area

Fieldwork was conducted in the Venezuelan Central coastal zone on the Mamo plateau, including hill slopes (5 - 20 m a.s.l.), situated in the Navy Base of Mamo district, Vargas State, in north Venezuela (10°36'N and 67°2'W). The expected vegetation type is a very dry tropical forest according to the climate regime of the Holdridge model [32]; however, some plant species from the tropical thorny shrubland also occur in the area (**Figure 1**), and for this reason Huber and Alarcon [33] classified vegetation as littoral xerophytic shrubland. The climate is characterized by two short precipitation peaks, the first between July and August, and the second between December and January. The total annual precipitation is 558 mm and the mean monthly temperature is 26.8°C [34]. Vegetation is represented by natural xerophytic shrubland, dominated by shrubs and herbs and a few small trees, which may reach five meters in height. The main plant families recorded in this area were Fabaceae, Poaceae, Asteraceae, Euphorbiaceae, and Cactaceae [34]. Fieldwork was carried out on a hill slope located close to the coastal zone, where the combined effects of rainfall intensity and steep



Figure 1. Study area. The lower part is a disturbed area and the upper part of the hill corresponds to an undisturbed area.

slopes produce soil erosion and, consequently, a discontinuous vegetation cover. Two successional types were evident according to the degree of disturbance. Disturbed areas were characterized mainly by perturbed soils and the development of vegetation comprising pioneer herbaceous species. In contrast, undisturbed areas, free of erosion or otherwise damaged by human activities, were dominated by long-lived woody species. Plant species were assigned to habitats during a census of the area.

2.2. Plant Species Selection and Phylogenetic Effect

The species investigated correspond to the area's flora recorded over three years by Castillo *et al.* [34] plus 11 additional plant species recorded during this study (N = 144). Formal phylogenetic analysis was not performed; however, to rule out the possible phylogenetic effect on the ecological patterns and associations found in the community, the frequency of sexual systems, dioecy, and monoecy were evaluated in relation to known plant clades [35] to provide an approximate indication of whether dioecy and monoecy are independent of phylogenetic lineages represented in the plant community. Additionally, it has been repeatedly demonstrated that the evolution of self-compatibility, self-incompatibility, and agamospermy are not phylogenetically constrained [36] [37] [38]. The liability of reproductive mode and life history in many plant families suggests that phylo-

genetic constraints rarely limit opportunities when ecological conditions require evolutionary shifts in the breeding system [39].

2.3. Functional Groups

All 144 plant species were characterized according to life form, succulence, dispersal syndrome and type of habitat occupied. Furthermore, pollination system specificity was established for 113 previously studied species.

Plant life forms were categorized according to habit, longevity, and stem lignification, height and ramification type. In the first instance, species were classified as perennial or short-lived. The life-span of herbaceous species was determined by observing a minimum of ten individuals per species over two years in both disturbed and undisturbed areas. Species in which more than 80% of individuals died during this period were considered short-lived or annual species. Species were also classified as succulents, having specialized fleshy tissue in a plant organ for the conservation of water, or non-succulents, and were further categorized according to the three main carbon assimilation pathways, C_3 , C_4 and CAM, following previously published data [30]. Additional information about carbon metabolism was obtained from the literature (see Appendix A). Species were also assigned to a successional status, based on where species grew in the community: 1) late seral or climax species, and 2) pioneer species. Late seral species grew in natural or undisturbed areas, while pioneer species occurred in disturbed areas, such as eroded sites, road edges, and water ponds constructed for domestic animals.

Observations on pollinators were made during three days of floral anthesis, and completed over three years of flowering periods. The activity of all types of floral visitors was described before visitors were captured. Pollinators were distinguished from other floral visitors using five criteria [40]: 1) presence of pollen, 2) if the body site where pollen is carried is available for pollination, 3) if pollen on the body of a vector could be transferred to a stigma (the pollen load made contact with the stigma during a visit), 4) relative abundance of each visiting species (if the relative abundance of each visiting species is significantly higher than zero), and 5) relationship between flower and visitor size. After that, plant species were categorized according to their pollination system specificity in relation to their pollen vectors (slightly modified from [41]). In this study, the following categories were used: 1) polyphyly—pollinated by different taxonomic orders of visitors, 2) oligophily—pollinated by more than one family of the same taxonomic order and 3) monophily—pollinated by only one species, one genus or different genera of the same taxonomic family. Occurrence of wind pollination was determined according to floral morphology [41] and in some cases, tested by enclosing flowers or inflorescences in 1 mm nylon mesh bags, which excluded most insects but allowed passage of airborne pollen [42].

Information on the morphological adaptation of dispersal units, fruits or seeds was obtained by field observations. Plants were classified according to four dispersal syndromes following Ramírez [9]: 1) abiotic dispersal, represented by

anemochorous (winged, dusted, balloons, plumed), ballists, and hydrochorous diaspores; 2) granivorous dispersal, represented by dry fruits and/or seeds, with or without elaiosome, dispersed by granivorous animals, including ants, birds, and mammals; 3) frugivory, diaspores dispersed by birds and mammals, including fleshy fruits and/or arilated seeds; and 4) epizoochory, diaspores adapted for transportation on the surface of animals, by having hooks, spines and/or sticky and mucilaginous surfaces.

2.4. Sexual Organization

The distribution of sexual organs in flowers, individual plants, populations, and species as well as their spatial separation and relative timing in the maturation of sexual organs in flowers, inflorescences or individual plants (**Table 1**) was determined for the total plant species recorded in the study area. Plant species were initially categorized according to sexual systems as hermaphroditic, andromonoecious, gynomonoeious, monoecious, subdioecious, or dioecious (see **Table 1** for the definition of reproductive terms), based mainly on floral morphology, including number ovule per ovary, information on literature specialized and functional criteria: experimental tests and fruit set. All hermaphroditic-dimorphic species were tested for cross- and self-pollination effectivity. On the basis of controlled crosses, fruit and seed sets, some morphologically hermaphrodite species were considered dioecious. In addition, morphologically hermaphroditic species were considered andromonoecious due to the absence of ovules in at least 20% of the flowers [9]. For comparative analyses, only three categories, hermaphrodite, monoecy (including andromonoecious and gynomonoeious species) and dioecy (including androdioecious, gynodioecious, and distylous-functional dioecious species) were considered.

Plant species were classified as herkogamous and non-herkogamous (**Table 1**). Spatial separation between pollen presentation and pollen receipt within flowers of hermaphrodite species and hermaphrodite functional-dioecious species or between flowers of monoecious taxa was measured. In this study, ordered herkogamy was determined when the stigma was positioned at a statistically significant separation from anthers [43]. The null hypothesis tested was if the mean separation between stigma-anther is equal to zero (no herkogamy).

Temporal variation in sexual expression was determined following Ramírez [9]. All hermaphroditic, submonoecious, monoecious and hermaphrodite functional-dioecious species were examined to establish if individual flowers or inflorescences (when treated as pollination units) had synchronous or asynchronous male and female phases [44]. In most species, synchrony of sexual expressions was evaluated by observations at 2-h intervals from the start of anthesis until flower or inflorescence senescence, in a minimum of ten flowers or inflorescences per species. Maturation of stamens was determined by anther dehiscence or, in the case of poricidal anthers, by the time when pollen could be dislodged from anthers. Female maturity was determined by a shiny or moist stigmatic surface in taxa with wet stigmas, or by the elongation of the style and full

development of the stigma in taxa with dry stigmatic surfaces. Plants were categorized as adichogamous (sexual synchrony, following [41], protandrous (anther dehiscence occurring before stigmatic receptivity), or protogynous (stigmatic receptivity prior to anther dehiscence). The latter two categories may include species with posterior overlapping of the sexual phases (incomplete dichogamy, sensu [44]).

2.5. Plant Breeding Systems

A total of 73 species were characterized in their breeding systems: 62 species were experimentally evaluated in this study, six species come from previous studies in the same study area and five additional species presented morphological and functional characteristics that correspond to species without spontaneous self-pollination and xenogamy. The occurrence of agamospermy was only tested for 60 species in the present study; six additional reports come from previous studies.

Reproductive efficiency under experimental conditions was determined at two levels: 1) fruits developed per total number of flowers, and 2) a total number of non-abortive seeds produced by all fruits per total number of ovules (flower number multiplied by the average number of ovules per flower). Experimental pollination tests considered in this study were: 1) agamospermy test, as fruits and/or seeds produced from emasculated and isolated flowers; 2) spontaneous self-pollination test, as fruits and/or seeds produced from isolated and non-manipulated flowers; 3) self-pollination test, as fruits and/or seeds produced from hand or assisted self-pollinated flowers; and 4) cross-pollination test, as fruits and/or seeds produced from hand outcrossed flowers. Nylon mesh bags were used to isolate flowers when this treatment was required. Breeding system data from previous studies in the same area for three Cactaceous species [25] [26], *Melochia pyramidata* var. *pyramidata* and *Melochia tomentosa* [27] and *Coccoloba uvifera* [45] were included in the general figure of plant community.

Four breeding system indexes (BSI) were determined at the fruit and/or seed level following [16]. Each BSI results from the quotient of two contrasting experimental tests, where the denominator is expected to be the largest referential value. In the case when the conclusion derived from both fruit and seed levels differed, it opted for the conclusion obtained at the seed level. Five categories for each breeding system index (Breeding Index Categories, BIC) were used [16] for all species: 1) $BSI = 0$, 2) $0 < BSI < 1.0$, 3) $BSI = 1.0$, 4) $0 < (1/BSI) < 1.0$ (when $BSI > 1.0$), and 5) $1/BSI \sim 0$ (when $BSI \sim \infty$). This system of categories is a symmetrical model at both sides of value 1.0, positioning contrasting categories at the extremes: 0 ($BSI = 0$) and ∞ ($1/BSI \sim 0$) values, which represent opposite biological conditions. Intermediate values, below ($0 < BSI < 1.0$) and above ($0 < (1/BSI) < 1.0$) 1.0, but lower than the extreme conditions, correspond to intermediate or transitional biological categories. $BSI = 1.0$ denotes the referential value indicating that the experimental tests conforming to the index render approximately equal results. More details about the categorization of the BSI, as-

sumptions and exceptional cases can be found in Ramírez and Nassar [16].

The Index of Agamospermy (IAG) was determined by dividing the results obtained from the agamospermy test by the results obtained from the cross-pollination test [46]; however, because reproductive efficiency of self- and cross-pollination tests may or may not be different in agamosperous species, the IAG had to be calculated on the basis of both cross- [IAG (cp)] and self-pollination [IAG (sp)] tests. Between the two, the index with the lowest value is the most appropriate one to be used, because it represents the comparison of agamospermy against the most efficient pollination test [16]. The Index of Spontaneous Self-Pollination (ISSP) or Automatic Self-pollination Index [47] [48] was determined by dividing reproductive efficiency from the spontaneous self-pollination test by reproductive efficiency obtained from the assisted self-pollination test. The Index of Self-Fertility (ISF) [49] was determined by dividing results from the spontaneous self-pollination test by results from the cross-pollination test. Finally, the Index of Self-Incompatibility (ISI) or Genetic Self-incompatibility Index [47] [48] was determined by dividing results from the hand self-pollination test by results from the cross-pollination test.

In addition, some zoophilous pollination species in which spontaneous self-pollination is avoided as a result of morphological traits, sexuality, and dichogamy, were considered as non-spontaneous self-pollination (BSI = 0). These were 1) plant species having pollen grouped into masses, pollinia, which have to be transported by pollinators from the androecium to the stigma (Asclepiadoideae in the Apocynaceae and Epidendroideae in the Orchidaceae), and 2) monoecious-herkogamous-dichogamous species, where unisexual flowers occur separately in time and space, without any possibility of spontaneous self-pollination (*Cnidocolus urens*). This approximation was confirmed by the very low fruit set under undisturbed conditions (N. Ramírez unpubl. data), which is an estimate of pollinator-mediated dependence on fruit production.

Information about flower number, fruit set and seed set under experimental pollination tests for 62 plant species belonging to 26 plant families is detailed in Appendix B. Agamospermy indexes for 66 plant species are reported in **Supplementary Material 1** and breeding system indexes and their qualitative categories for 73 species are reported in **Supplementary Material 2**.

2.6. Statistical Analysis

The t-test was employed to determine corresponding breeding system categories for the four indexes of each plant species. T-test, with degrees of freedom equal to $n - 1$ [50] was used to discriminate between Breeding System Index (BSI) values from 0 and 1.0 (see [16] for details). When BSI values were higher than ≥ 1.0 (up to infinite), the inverse value ($1/BSI$) was used instead of BSI, to make the statistical method symmetrical at both sides of $BSI = 1$. In order to calculate the four BSI that make the composite breeding system of a given species using fruit set or seed set data, the user can have access to an Excel spreadsheet that automatically calculates

all the parameters described above when fruit or seed set data are entered in the appropriate cells. This Excel file can be provided by the authors upon request or visiting the website <http://jafetnassar.wixsite.com/compositebs>.

Log-linear analyses of frequency using two-way tables to determine dependence between reproductive (sexual system, dichogamy, herkogamy, and breeding system) and functional (life form, carbon metabolism, successional stages, pollination system, and dispersal syndrome) attributes were used. For example, comparing sexual systems and habitats, the frequencies of hermaphrodite, monoecious, and dioecious species that occurred in undisturbed and disturbed habitats were contrasted. In order to establish the level of dependence between reproductive variables and functional groups, log-linear analyses of frequency were performed using two-way tables [51]. The concept of interaction in log-linear analyses is analogous to that used in the analysis of variance. When the log-linear analysis of frequency was significant, residual frequencies (*i.e.*, observed minus expected frequencies) were estimated for each cell of the two-factor comparison, and then standardized and tested for significance. This analysis established which pairs of variables deviated significantly from expected values [52], and therefore, made a larger contribution to the association. Significant and positive residuals indicated a strong association between both categories, and significant and negative residuals indicated an unusual occurrence.

3. Results

3.1. Sexual System and Taxonomy

Information on plant species, taxonomic position, sexual systems, dichogamy, herkogamy, and habitats is compiled in Appendix A. Of the 144 plant species studied, 72.9% were hermaphroditic, 22.9% monoecious, and 4.2% dioecious (Table 2). Dioecious species ($N = 6$) recorded belong to three clades [35] and five plant families: Campanulids ($N = 1$, from Asteraceae), Lamids ($N = 2$, from Boraginaceae), and Malvids ($N = 1$, from Nyctaginaceae; $N = 1$, from Polygonaceae; and $N = 1$, from Santalaceae). The clades represented had different life forms: Campanulids and Lamids are perennial herbs, shrubs and lianas, while the Malvids are shrubs, trees, and perennial herbs. Monoecious species ($N = 33$) belong to five different clades: Fabids, Malvids, Campanulids, Commelinids, and Lamids [35] and exhibited all life forms, trees, shrubs, lianas, perennial herbs, and annual herbs. Fabids represented the largest clades ($N = 17$) and included also the five life forms, trees ($N = 1$), shrubs ($N = 3$), liana ($N = 1$), perennial herbs ($N = 6$), and annual herbs ($N = 6$). The rest of the species are hermaphrodites belonging to 33 plant families. Monoecy was represented by 13.2% ($N = 19$) of monoecious species with exclusively unisexual flowers, 7.6% ($N = 11$) andromonoecious, and 2.2% ($N = 3$) gynomoecious taxa. Most dioecious species were morphologically hermaphrodites with functional dioecy (3.5%; $N = 5$) and only one species (0.7%) had morphologically unisexual flowers. Plant sexual systems varied as a function of the successional stage: dioecy was higher in the

Table 2. Frequency of sexual system, temporal sexual expression, and spatial sexual separation according to some functional plant traits and seral states of the xerophytic shrubland.

| Functional group and plant communities | Sample size | Sexuality | | | Temporal variation between sexual expression | | | Spatial separation between pollen-stigma | |
|--|-------------|-------------------------------------|-----------|----------|--|-----------|-----------|--|---------------|
| | | Hermaphrodite | Monoecy | Dioecy | Adichogamy | Protandry | Protogyny | Herkogamy | Non-Herkogamy |
| | | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) |
| Life form | | df = 8; $\chi^2 = 4.3$ (n.s.) | | | df = 8; $\chi^2 = 12.7$ (n.s.) | | | df = 4; $\chi^2 = 5.8$ (n.s.) | |
| Trees | 14 | 11 (78.6) | 2 (14.3) | 1 (7.1) | 9 (69.2) | 4 (30.8) | 0 (0.0) | 12 (92.3) | 1 (7.7) |
| Shrubs | 28 | 21 (75.0) | 5 (17.9) | 2 (7.1) | 21 (80.8) | 5 (19.2) | 0 (0.0) | 21 (80.8) | 5 (19.2) |
| Lianas | 20 | 15 (75.0) | 4 (20.0) | 1 (5.0) | 15 (75.0) | 4 (20.0) | 1 (5.0) | 16 (84.2) | 3 (15.8) |
| Perennial herbs | 43 | 29 (67.4) | 12 (27.9) | 2 (4.7) | 26 (63.4) | 9 (22.0) | 6 (14.6) | 27 (65.8) | 14 (34.2) |
| Annual herbs | 39 | 29 (74.4) | 10 (25.6) | 0 (0.0) | 21 (53.8) | 9 (23.1) | 9 (23.1) | 27 (69.2) | 12 (30.8) |
| Succulence | | df = 2; $\chi^2 = 1.8$ (n.s.) | | | df = 2; $\chi^2 = 2.1$ (n.s.) | | | df = 1; $\chi^2 = 0.4$ (n.s.) | |
| Non-succulent | 115 | 85 (70.8) | 30 (25.0) | 5 (4.2) | 77 (66.4) | 24 (20.7) | 15 (12.9) | 87 (75.6) | 28 (24.4) |
| Succulent | 23 | 20 (83.3) | 3 (15.5) | 1 (4.2) | 15 (65.2) | 7 (30.4) | 1 (4.4) | 16 (69.6) | 7 (30.4) |
| Carbon metabolism | | df = 4; $\chi^2 = 6.6$ (n.s.) | | | df = 4; $\chi^2 = 6.3$ (n.s.) | | | df = 2; $\chi^2 = 1.9$ (n.s.) | |
| C ₃ | 97 | 70 (72.2) | 21 (21.6) | 6 (6.2) | 65 (70.6) | 18 (19.6) | 9 (9.8) | 71 (78.0) | 20 (22.0) |
| C ₄ | 29 | 19 (65.5) | 10 (34.5) | 0 (0.0) | 17 (58.6) | 6 (20.7) | 6 (20.7) | 19 (65.5) | 10 (34.5) |
| CAM | 18 | 16 (88.9) | 2 (11.1) | 0 (0.0) | 10 (55.6) | 7 (38.9) | 1 (5.4) | 13 (72.2) | 5 (27.8) |
| Dispersal syndromes ^Δ | | df = 6; $\chi^2 = 17.5$, P < 0.007 | | | df = 6; $\chi^2 = 10.1$ (n.s.) | | | df = 3; $\chi^2 = 1.9$ (n.s.) | |
| Frugivory ¹ | 40 | 30 (75.0) | 5 (12.5) | 5 (12.5) | 27 (75.0) | 7 (19.4) | 2 (5.6) | 28 (80.0) | 7 (20.0) |
| Granivorechory ² | 59 | 34 (64.2) | 19 (35.8) | 0 (0.0) | 32 (60.4) | 10 (18.9) | 11 (20.7) | 37 (69.8) | 16 (30.2) |
| Abiotic ³ | 43 | 27 (62.8) | 14 (32.6) | 2 (4.6) | 21 (51.2) | 14 (34.2) | 6 (14.6) | 33 (80.5) | 8 (19.5) |
| Epizoochory | 18 | 16 (88.9) | 2 (11.1) | 0 (0.0) | 14 (77.8) | 3 (16.7) | 1 (5.5) | 13 (72.2) | 5 (27.8) |
| Pollination systems | | df = 6; $\chi^2 = 11.8$ (n.s.) | | | df = 6; $\chi^2 = 6.8$ (n.s.) | | | df = 3; $\chi^2 = 2.1$ (n.s.) | |
| Monophily | 24 | 21 (87.5) | 3 (12.5) | 0 (0.0) | 18 (75.0) | 4 (16.7) | 2 (8.3) | 20 (83.3) | 4 (16.7) |
| Oligophily | 28 | 24 (85.7) | 4 (14.3) | 0 (0.0) | 24 (85.7) | 3 (10.7) | 1 (3.6) | 24 (85.7) | 4 (14.3) |
| Polyphily | 44 | 28 (63.6) | 12 (27.3) | 4 (9.1) | 25 (61.0) | 13 (31.7) | 3 (7.3) | 30 (75.0) | 10 (25.0) |
| Anemophily | 17 | 11 (64.7) | 6 (35.3) | 0 (0.0) | 10 (58.8) | 5 (29.4) | 2 (11.8) | 12 (70.6) | 5 (29.4) |
| Habitats | | df = 2; $\chi^2 = 5.11$ (n.s.) | | | df = 2; $\chi^2 = 1.43$ (n.s.) | | | df = 1; $\chi^2 = 1.05$ (n.s.) | |
| Late seral (undisturbed) | 45 | 34 (75.6) | 7 (15.5) | 4 (8.9) | 26 (61.9) | 12 (28.6) | 4 (9.5) | 33 (80.5) | 8 (19.5) |
| Pioneer (disturbed areas) | 99 | 71 (71.7) | 26 (26.3) | 2 (2.0) | 66 (68.0) | 19 (19.6) | 12 (12.4) | 70 (72.2) | 27 (27.8) |
| Overall community | 144 | 105 (72.9) | 33 (22.9) | 6 (4.2) | 92 (66.2) | 31 (22.3) | 16 (15.5) | 103 (74.6) | 35 (25.4) |

^Δ: ¹ = Birds, mammals (including bats), and/or reptiles; ² = Birds, mammals and/or ants; ³ = Abiotic = wind, water, and/or ballistic dispersal. The number of dispersal syndromes exceeds the number of plant species (N = 144) because some species have more than one dispersal syndrome.

late seral than the pioneer stage, and the opposite was true for monoecy.

3.2. Herkogamy and Dichogamy

Adichogamy (N = 91; 65.94%) was better represented than dichogamy (N = 47; 34.06%) in hermaphrodite and monoecious species; protandry was more frequent than protogyny (Table 3). Herkogamous-adichogamous species accounted for 66.69% of herkogamous species. The percentage of protandrous species was higher in undisturbed than disturbed habitats. Overall, the frequency of herkogamous species was higher than non-herkogamous species, but non-herkogamy was better represented in disturbed than undisturbed habitats (Table 2). The relationship between temporal variation in sexual expression and herkogamy was not significant (d.f. = 2, $\chi^2 = 3.5$, n.s.), despite the fact that most herkogamous species were adichogamous, followed by protandrous and protogynous, respectively (Table 3).

The relationship between sexual system and herkogamy was not significant (d.f. = 1, $\chi^2 = 0.8$, n.s.), though hermaphrodite (N = 79; 57.2%) and monoecious (N = 24; 17.4%) species were mostly herkogamous (see Table 3). Temporal variation in sexual expression and sexual system (hermaphrodite and monoecy only) were significantly associated (d.f. = 2, $\chi^2 = 47.6$, P = 0.0000). Hermaphrodite species were mostly adichogamous (N = 84; 80.0%). In contrast, most monoecious species were dichogamous (N = 26; 78.8%). Protandry and protogyny occurred in identical frequencies (N = 13; 39.4% each one), and only 21.2% of species (N = 7) were adichogamous (Table 3).

Table 3. Multiple response table of sexual systems (hermaphrodite and monoecy) and temporal and spatial separation of sexual expression of 138 hermaphrodite and monoecious species from the xerophytic shrubland.

| Sexuality | Herkogamy | Adichogamy | Protandry | Protogyny | Total row ¹ |
|---------------------------------|---------------|------------|------------|------------|------------------------|
| | | N (%) | N (%) | N (%) | N (%) |
| Hermaphrodite | Herkogamy | 63 (79.75) | 16 (20.25) | 0 (0.00) | 79 (57.24) |
| Monoecy | Herkogamy | 6 (25.00) | 9 (37.50) | 9 (37.50) | 24 (17.39) |
| Total Herkogamy | | 69 (66.69) | 25 (24.27) | 9 (8.74) | 103 (74.64) |
| Hermaphrodite | Non-herkogamy | 21 (80.77) | 2 (7.69) | 3 (11.54) | 26 (18.84) |
| Monoecy | Non-herkogamy | 1 (11.11) | 4 (44.44) | 4 (44.44) | 9 (6.52) |
| Total non-herkogamy | | 22 (62.86) | 6 (17.14) | 7 (20.00) | 35 (25.36) |
| Total Monoecy | | 7 (21.21) | 13 (39.39) | 13 (39.39) | 33 (23.91) |
| Total Hermaphrodite | | 84 (80.00) | 18 (17.14) | 3 (0.95) | 105 (76.09) |
| Total (hermaphrodite + monoecy) | | 91 (65.94) | 31 (22.46) | 16 (11.59) | 138 |

Percentages are based upon the total number of plant species for each row. ¹Percentage determined upon 138 plant species.

3.3. Sexual Organization and Functional Groups Associated

Sexual systems and attributes associated. Plant sexual system was only significantly associated with seed dispersal syndromes (**Table 2**). Granivorechory and abiotic dispersal was the most frequent seed dispersal syndrome in monoecious species. Seed dispersal mediated by frugivory was the main syndrome found in dioecious plants. In spite of a non-significant association, the proportion of dioecious species was higher in plants with polyphilous pollination and late seral stage. Monoecy tended to be higher for herbaceous species, non-succulent plants, anemophilous and polyphilous pollination systems and pioneer seral stage.

Temporal variation in sexual expression did not exhibit significant relation with functional traits (**Table 2**); however, the proportion of protogyny was higher for herbaceous species, non-succulent, C_4 species and dispersed by granivores animals. In contrast, protandrous taxa were abiotically dispersed, and polyphilous and anemophilous pollination.

Herkogamy was not significantly associated with functional traits (**Table 2**); however, non-herkogamous species tend to be mostly herbaceous species, dispersed by granivorechory and epizoochory, polyphilous and anemophilous pollination, and frequently found in disturbed areas.

3.4. Plant Breeding Systems

Most plant species studied were non-agamospermous ($N = 61$; 92.4%) and 7.6% ($N = 5$) were partially agamospermous (see **Table 1** for the definition of reproductive terms). These proportions were comparable for undisturbed and disturbed habitats. Partially agamospermous species were most numerous for herbaceous species from disturbed areas (**Supplementary Material 3; Figure 2**).

The five possible categories of the Index of Spontaneous Self-Pollination (ISSP) were recorded in the sample studied (see **Table 1** for the definition of reproductive terms). Most species presented partially spontaneous self-pollination (46.6%), followed by non-spontaneous self-pollination (37.0%), partially constrained assisted self-pollination (13.6%), spontaneous self-pollination (*Rhynchosia minima*) and obligated spontaneous self-pollinated (*Jacquemontia cumanensis*) (**Supplementary Materials 2, 3**). However, obligated spontaneous self-pollination in *Jacquemontia cumanensis* was represented by a small fraction of flowers producing fruits and seeds by self-pollination (**Supplementary Material 2**).

Some trends for spontaneous self-pollination categories and functional groups were observed: non-spontaneous self-pollinated species corresponded to trees and lianas, followed by shrubs and perennial herbs, and only one species was an annual herb (*Phyllanthus niruri*). A substantial fraction of non-spontaneous self-pollinated species grows in undisturbed areas of the shrubland. Partially spontaneous self-pollinated species were annual herbs, polyphilous, growing in disturbed areas. Species with partially constrained assisted self-pollination were more frequent among herbs growing in disturbed areas.

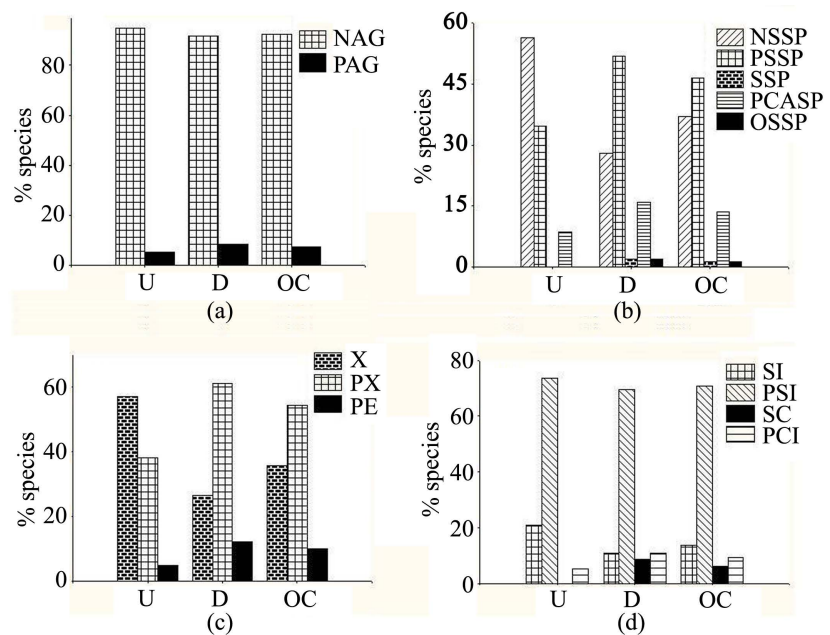


Figure 2. Frequency distribution of breeding system categories according to undisturbed habitat (U), disturbed habitat (D) and overall community (OC). Agamospermy index categories (a): NAG = no agamospermy, PAG = partially agamospermy. Spontaneous self-pollination index categories (b): NSSP = not spontaneous self-pollination, PSSP = partial spontaneous self-pollination, SSP = spontaneous self-pollination, PCASP = partial constrained assisted self-pollination, OSSP = Obligated spontaneous self-pollination. Self-fertility index categories (c): X = xenogamy, PX = partial xenogamy, PE = partial endogamy. Self-incompatibility index categories (d): SI = self-incompatibility, PSI = partial self-incompatibility, SC = self-compatible, PCI = partial cross-incompatibility.

Three categories of the Index of Self-fertility (ISF) were recorded: xenogamous ($N = 25$), partially xenogamous ($N = 38$), and partially endogamous ($N = 7$) (**Supplementary Information 3**) (see **Table 1** for the definition of reproductive terms). The highest frequency of xenogamy was found in trees and lianas; a large proportion of xenogamous species are dispersed by frugivorous animals. More than 50% of the xenogamous species grow in undisturbed areas. Partially xenogamous taxa were mostly shrubs and herbs found in disturbed areas and undergo polyphilous pollination. Partially endogamous species were herbs, mostly dispersed by granivorechory and epizoochory and grow in disturbed areas (**Supplementary Information 3, Figure 2**).

Four categories of the Index of Self-incompatibility (ISI) were found in the sample examined: partially self-incompatible ($N = 46$), self-incompatible ($N = 9$), partially cross-incompatible ($N = 6$), and four plant species were completely self-compatible (see **Table 1** for the definition of reproductive terms). The relationship between the ISI categories and functional groups are detailed in **Supplementary Information 3**. Trees and lianas were predominantly self-incompatible from undisturbed areas. Partial cross-incompatibility was found in six predominantly herbaceous species, dispersed abiotically or by granivorous animals and growing mostly in disturbed areas.

3.5. Breeding Systems and Sexual Organization

The relationships between sexual organization and breeding systems were not significant, except for the self-fertility index categories and dichogamy (Table 4). Regardless of non-statistical relationships, the sexual organization showed that most plant species examined were similarly distributed across the breeding system indexes for hermaphrodite, herkogamous and adichogamous species; however, frequencies of non-spontaneous self-pollinated-protogynous and partially spontaneous self-pollinated-protandrous species were relatively higher than their respective counterparts. In addition, non-spontaneous self-pollination was more frequent than partially spontaneous self-pollination for monoecious taxa. Xenogamous and partially xenogamous species were mostly adichogamous; however, frequencies of xenogamous-protogynous and partially xenogamous-protandrous species were relatively higher than their respective counterparts. Self-incompatibility was recorded in slightly higher frequency than partial self-incompatibility for adichogamous and herkogamous species. Protandry

Table 4. Relationship between the most common breeding system index categories and morphological and temporal organization sexual traits.

| Breeding system | Sexuality | | Spatial separation between pollen-stigma | | Temporal variation between sexual expression | | |
|--|-------------------------------|-----------|---|-----------------|---|-----------|-----------|
| | Hermaphrodite | Monoecy | Herkogamous | Non-Herkogamous | Adichogamy | Protandry | Protogyny |
| | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) |
| Agamospermy index categories | NA | | NA | | NA | | |
| Non-agamospermy | 47 (79.7) | 12 (20.3) | 45 (75.0) | 15 (25.0) | 43 (71.7) | 10 (16.7) | 7 (11.6) |
| Spontaneous self-pollination index categories | $\chi^2 = 1.2$, df = 1, n.s. | | $\chi^2 = 0.01$, df = 1, n.s. | | $\chi^2 = 4.3$, df = 2, n.s. | | |
| Non-spontaneous self-pollination | 20 (76.9) | 6 (22.1) | 21 (80.8) | 5 (19.3) | 19 (70.4) | 2 (7.4) | 6 (22.2) |
| Partial spontaneous self-pollination | 29 (87.9) | 4 (12.1) | 27 (81.8) | 6 (18.2) | 25 (75.8) | 6 (18.2) | 2 (6.0) |
| Self-fertility index categories | $\chi^2 = 0.01$ df = 1, n.s. | | $\chi^2 = 0.01$ df = 1, n.s. | | $\chi^2 = 7.9$, df = 2, P < 0.019 | | |
| Xenogamys | 20 (83.3) | 4 (16.7) | 18 (75.0) | 6 (25.0) | 20 (80.0) | 1 (4.0) | 4 (16.0) |
| Partially xenogamy | 31 (83.8) | 6 (12.2) | 28 (75.7) | 9 (24.3) | 26 (70.3) | 10 (27.0) | 1 (2.7) |
| Self-incompatibility index categories | $\chi^2 = 0.1$, df = 1, n.s. | | $\chi^2 = 0.3$, df = 1, n.s. | | $\chi^2 = 2.4$, df = 2, n.s. | | |
| Self-incompatibility | 37 (86.1) | 6 (13.9) | 33 (86.8) | 5 (13.2) | 8 (88.9) | 1 (11.1) | 0 (0.0) |
| Partial self-incompatibility | 9 (81.8) | 2 (18.2) | 13 (81.3) | 3 (18.7) | 31 (67.4) | 5 (10.9) | 10 (21.7) |

NA = Statistical tests were not performed.

occurred in a similar frequency for self-incompatible and partially self-incompatible species. In contrast, protogyny was only found in partially self-incompatible species.

4. Discussion

The reproductive traits and their associations with functional groups allowed us to know the types and diversity of forms of sexual reproduction in species adapted to extreme environments. In addition to the main morphological and physiological adaptations frequently indicated for xerophytic species, the main reproductive trends found in the xerophytic shrubland were high levels of outbreeding strategies in woody species dispersed by frugivores from undisturbed areas, mixed breeding strategies occurred in disturbed areas and overall community, and inbreeding strategies in mostly herbaceous life forms, dispersed by all dispersal syndromes, primarily from disturbed areas. The ecological significance of the results obtained in the context of plant ecology and biodiversity is related to the structure of the vegetation, extreme climatic conditions, recurrent soil disturbances and the relatively low diversity of species. The associations between reproductive systems and functional groups provide ecological information on the occurrence of particular reproductive strategies present in functional groups and their importance in extreme environments, the r-K strategies of the species. The comparative analysis of the reproductive systems between different communities allows us to show how the ecological conditions and biodiversity of the xerophytic shrubland are related to the ecology and evolution of the reproductive systems of undisturbed and disturbed environments.

The most outstanding aspects of functional diversity in the xerophytic community are: 1) Functional diversity may be a response to ecological characteristics of the community (climatic regime, low species richness, shrubland structure, and disturbance) that produce specific ecological relationships. 2) The functional diversity of the xerophytic shrub community may be associated with different habitats: natural and anthropic disturbances produce various types of environments associated with different reproductive strategies and seed dispersal modes. 3) The types and diversity of reproductive systems in the xerophytic community with extreme conditions and a bushy structure present some similar reproductive characteristics found in much more diverse plant communities and with less extreme environmental conditions. It is likely that convergences in reproductive attributes may respond, among many other variables, to regional or latitudinal patterns.

4.1. Sexual Systems

The frequency distribution of sexual systems in the xerophytic shrubland is concordant with results shown for many tropical communities [5] [6] [7] [9] [12] [23] [53] [54] [55] [56] [57] and others), irrespectively of climate. Dioecy is mainly related to the woody condition, generalist pollination systems and seed dispersal by frugivores [8] [9] [23] [56] [58] [59] [60] [61] [62]. Only seed dis-

persal by frugivores was found to be significantly associated with dioecy in the xerophytic shrubland, as previously recorded [7] [9] [63]. The presence of fleshy fruit in dioecious species is only one element in the occurrence of dioecy in the xerophytic shrubland. Likewise, dioecy tends to be related to polyphilous pollination systems, which is consistent with the general relations of dioecious species. Despite non-association between life form and sexual system, the low proportion of dioecious species in this xerophytic shrubland is similar to tropical shrublands in the Gran Sabana Plateau [5] [54], overall heterogeneous vegetation units in the Venezuelan Central Plain [9], and under stressing conditions [15]. Interestingly, in the xerophytic shrubland, dioecy was more than four times higher in the late seral state than in the pioneer state. The low number of dioecious species in the latter may be related to predominantly herbaceous species occurring in disturbed areas generated by anthropogenic activity and by the effect of rainfall driven soil erosion and runoff, a common phenomenon in arid environments [3]. Dioecy is found in very low frequency in disturbed areas in some tropical communities [5] [9], because of the high number of colonizing herbaceous species and the well-recognized association between the woody condition and dioecy.

Monoecy promotes cross-pollination by preventing within-flower selfing [58] [64] [65]. The proportion of monoecious species in undisturbed habitats (15.5%) found here is close to that in the mesothermic shrublands of the Gran Sabana Plateau (14%; [5], secondary deciduous forest remnant (18.7%; [7], and psamphyllous (17.2%) and littoral meadows (13.9%) in the coastal plains of the Paraguaná Península [12]. This highlights two attributes influencing monoecy in undisturbed xerophytic shrublands: vegetation structure and dry coastal climate. In contrast, disturbed habitats exhibited a comparatively higher frequency of monoecious species (26.3%) related to the high number of herbaceous species. This figure suggests that permanent disturbance caused by humans and the natural erosion process may select monoecy as the main figure for cross-pollination throughout increment of herbaceous colonizing species. The high proportion of monoecy observed in disturbed habitats may be associated with the xerophytic environment, where the stressful condition is caused by water deficit. Separate sexes are favored in stressful environments [8] [10] [58] [59] [66] [67]. Division of function in unisexual plants may increase male and female fitness due to a compensation effect [28], unless physiological constraints are so severe as to generate low plant density or lack of pollinators or reduced fertility. The association between monoecy colonizing species and C_4 carbon metabolism may enhance the capacity of herbaceous- C_4 species to reduce water loss in water limiting environments [68].

The high proportion of submonoecy found among monoecious species examined agrees with the results found in the Gran Sabana Plateau [5], and in the Venezuelan Central Llanos [9], and suggests that, in many cases, monoecy might have evolved from hermaphroditism. Male flowers in andromonoecous species may enhance male fitness by increasing pollen amount and pollen dispersal in

the population and subsequently pollination efficiency, needed for many andromonoecious-polyphilous and -anemophilous species in the shrubland, where pollen required may be fulfilled by pollen produced by male flowers. In addition, seed dispersal by granivores and wind in monoecious-herbaceous species represents associations frequently found in herbs growing in disturbed areas [9] [24]. These dispersal syndromes may be considered opportunistic dispersal strategies for plant species colonizing disturbed habitats in the xerophytic shrubland where perturbations are continuous.

4.2. Herkogamy and Dichogamy

Herkogamy was twice as often as dichogamy in the xerophytic shrubland. A similar result has been reported in three other Venezuelan plant communities with contrasting species compositions and structures [5] [6] [7] [9]. The parallelism in the frequency of dichogamy and herkogamy observed between different geographic areas and plant communities, suggests convergent evolution in mechanisms that help avoid pollen-stigma interference and promote cross-pollination, irrespective of the taxonomic composition and ecological characteristics of plant communities. In the xerophytic shrubland, the frequency of dichogamy and herkogamy was not significantly associated with functional groups; however, there were some important trends, including disturbance. Herkogamy is a critical strategy for outcrossing in undisturbed xerophytic shrubland, but has slightly less importance in disturbed areas. These associations are concordant with a number of mechanisms that promote cross-pollination in late seral stages, mainly woody species [9] [24]. The abundance of non-herkogamous species in herbaceous and disturbed areas suggests that selfing strategies may represent an important adaptation for autogamous colonizing species, mostly granivore-chorous dispersal and polyphilous and anemophilous pollination.

Several surveys indicate that protandry is more common than protogyny [5] [7] [9] [69]. The proportion of protandry was approximately two times the proportion of protogyny in an extensive survey of intra-floral dichogamy [70]. In the xerophytic shrubland, the frequency of protandry was 1.4 times the frequency of protogyny, which is less than the ratio found in the Venezuelan Central Plain [9] and herbaceous-shrubby communities in the Gran Sabana plateau [5]. The frequency of protandry and protogyny was dependent on the successional stage found in the xerophytic shrubland: the highest protandry/protogyny ratio was noteworthy in primary vegetation (3.0), compared to disturbed vegetation (1.6). Protandry may act as a non-rigid mechanism in the undisturbed xerophytic shrubland and suggests a more versatile way of allogamy or a mixed-breeding system under environments characterized by low precipitation and high temperatures. Additionally, the highest frequency of protandry in the undisturbed xerophytic shrubland was non-significantly associated with abiotic dispersal and polyphily and anemophily pollination system. In this context, Barrett [71] pointed out that dichogamy is an exceptional widespread floral strategy occurring in many outcrossing species, regardless of the pollination system, which

partially agrees with our results.

4.3. Sexual Organization Associations

The sexual system, herkogamy and dichogamy may be in such a combination that each other's partial effectiveness is reinforced, cross-pollination promoted and pollen-stigma interferences avoided. For instance, the presence of dichogamy associated with herkogamy in the xerophytic shrubland represents a significant fraction (74.64%), similar to that found in the herbaceous-shrubby communities in the Gran Sabana Plateau [5]. Herkogamous-dichogamous species avoid self-pollination and may be considered the first step in the evolution of delayed selfing to provide reproductive assurance [72]. Hermaphrodite-herkogamous species tend to promote cross-pollination through herkogamy (79.8%) and less frequently through dichogamy (20.2%) in the xerophytic shrubland, similar to that found in the herbaceous-shrubby communities in the Gran Sabana Plateau [5]. Such outcomes show that sexual organization promote cross-pollination and avoids pollen-stigma interference in the xerophytic shrubland, and there is only a small proportion of plant species without adaptation for cross-pollination, represented by adichogamous-non-herkogamous species.

4.4. Plant Breeding Systems

The majority of species examined in the xerophytic shrubland were non-agamospermous. This pattern is consistent with the observed limited occurrence of agamospermy at the community level in many ecosystems [6] [7] [19] [36], with available records at the family level [73], and others [16]. Only 7.6% of plant species were partially agamospermous, which is equivalent to facultative agamospermy. This proportion is less than levels found in some isolated tropical communities [5] [18] and larger or similar to other tropical areas [12] [19] [74]. The occurrence of partially agamospermous species tends to be associated with herbaceous life forms growing mainly in disturbed areas [74]. The highest frequency of partially agamospermous species has been found in disturbed areas [5] [48]. Accordingly, herbaceous life form and disturbance may be considered central factors modeling the incidence of partial agamospermy in the xerophytic shrubland where conditions are mainly uncertain for reproduction.

Trends of breeding system categories observed in the xerophytic shrubland and patterns recorded for species established in late seral and disturbed areas, matched those reported in the herbaceous-shrubby communities in the Gran Sabana Plateau [5]. The most frequent breeding system categories were partial spontaneous self-pollination, partial xenogamy and partial self-incompatibility in overall community and disturbed areas. Most of these categories exhibited generalized life-history strategies, mostly well-represented by herbs growing in disturbed areas; the largest parts of these are recognized pioneer species [13] [75]. Probably, recurrent disturbance and the abundance of herbaceous species in the steep areas of the xerophytic shrubland are also related to the predom-

ance of mixed breeding strategies, in addition to the association with the high frequency of polyphilous pollination systems. The greatest proportion of species recorded in our study was partially self-incompatible. Partial self-incompatibility has been interpreted as evidence of high reproductive success, associated with mixed-breeding under the current scenario of pollination service in natural ecosystems [76], and 56 it is considered an optimal and evolutionary stable breeding strategy [77]. The frequency of partially self-incompatible species was similar in undisturbed and disturbed areas of the xerophytic shrubland; a larger than that recorded in the herbaceous-shrubby communities in the Gran Sabana Plateau [5]. Partial self-incompatibility and shrub and herb association in the xerophytic shrubland could bias the occurrence of partially self-incompatible species in undisturbed and disturbed areas.

The second most important frequency of non-spontaneous self-pollination and xenogamy in the xerophytic shrubland were correlated with specialized life history strategies: woody and perennial life forms from undisturbed areas, which are primarily related with the high incidence of xenogamy in woody species [5] [7] [78]. Additionally, a large proportion of xenogamous species are dispersed by frugivorous animals. Frugivory in xenogamous species is associated with late seral stages, where plant species have specialized reproductive strategies [22] [24]. Self-incompatibility was the second most significant category and similar to that found in the mesothermic shrublands [5]. Life form composition seems to be related with self-incompatibility frequency in the xerophytic shrubland. Trees and lianas tend to be predominantly self-incompatible in undisturbed areas, which agree with the recognized association between self-incompatibility and woodiness [5] [21] [60]. Woody life form may influence self-incompatibility occurrence, because perennial life history is generally associated with multiple reproductive episodes and consequently with the permanent contribution to reproductive success.

Among inbreeding strategies, a low frequency of partial constrained assisted self-pollination, partial endogamy and partial cross-incompatibility were recorded in disturbed areas and the overall community. Most of these species were herbs, dispersed by granivorechory and epizoochory, and growing in disturbed areas; the largest parts of these are pioneer species [13] [76]. Partial endogamy may occur under a variety of conditions, being more frequent for taxa growing in stressful environments, with reduced pollinator service [11] [12] [13], and with some specific traits, such as invasive-exotic or colonizing species [79] [80]. Herbaceous life forms and generalist dispersal syndromes suggest that partially endogamous species may be influenced by flexible reproductive attributes, mainly in herbaceous pioneer species in xeric environments.

Cross-incompatibility is a breeding system category poorly examined at the community level [16]. Partial cross-incompatibility was found in six predominantly herbaceous species, dispersed abiotically and by granivorous animals, and growing mostly in disturbed areas in the xerophytic shrubland, with frequency comparatively low to that found in the mesothermic shrublands (23% - 31%,

[5]). Ecological circumstances also play an important role in determining when selfing evolves [81]. Seed dispersal by granivorous animals or wind together with herbaceous life form could relate to inbreeding in some taxa from disturbed areas in the xerophytic shrubland, as has been recorded in a secondary deciduous forest remnant [7].

4.5. Sexual Organization and Breeding Systems

Most of the plant species were similarly distributed among breeding system categories for hermaphrodite, herkogamous and adichogamous species. Most of the herkogamous species were similarly distributed for spontaneous self-pollination index categories, self-fertility index categories, and self-incompatibility index categories (see **Table 1** for the definition of reproductive terms) and suggest that herkogamy is the main floral attribute avoiding autogamy in this plant community such as reported previously [5] [6] [7] [82]. In contrast, dichogamy, protandry and protogyny, have a differential role in promoting cross-pollination and avoiding pollen-stigma interference. Protogynous species tend to be xenogamous while protandrous species are predominantly partially xenogamous, proposing that protogyny could be a more effective attribute than protandry to avoid pollen-stigma interference. Self-incompatibility and partial self-incompatibility were mostly associated with hermaphroditism, herkogamy, and adichogamy, which agrees with previous studies [5] [6] [7] [17], though dichogamy, has been found equally common among self-incompatible and self-compatible species [70]. However, protogyny was only found in partially self-incompatible species. This figure represents attributes that can promote cross-pollination in plant species where self-pollination is possible.

5. Conclusion

Outbreeding and inbreeding strategies and mixed breeding strategies documented in this study only exhibited some associations with functional groups and disturbance. Sexual systems were only associated with dispersal syndromes and dichogamy and herkogamy. Taxonomic diversity and ecological variation in plant life forms within and between clades suggest that dioecy, monoecy and diclinous sexual systems are not conditioned by a phylogenetic effect, or their influence should be considered negligible. The specific meaning of the reproductive systems found in the xerophytic community in the context of plant ecology and biodiversity is as follows: 1) The high levels of species with outbreeding strategies, obligate or partially obligate interbreeding systems, with obligatory cross-pollination for reproduction success and high levels of genetic diversity are associated with trees from undisturbed areas and dispersed by frugivores, which suggests that long-lived woody species, K-strategy, are dispersed over long distances by animals and have particular adaptations to produce fleshy fruits despite the water limitations of the xerophilous shrubland. Long-distance dispersal is an important condition in species with obligatory cross-pollination. 2) Mixed

reproductive systems in species from disturbed areas and the overall community represent combined reproductive strategies and variable levels of outbreeding and genetic variability in the progeny. These species are dispersed by all dispersal types and are associated with different successional conditions, suggesting variable life strategies in species with mixed reproductive systems. 3) Inbreeding strategies were associated with mostly herbaceous life forms primarily in disturbed areas, which shows that a low number of species in disturbed areas are independent of cross-pollination for their reproduction and that self-pollination guarantees reproductive success; a typical colonizing strategy, r-strategy, of areas where the availability of pollinators may be limited.

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Author Contributions

The corresponding author is the only responsible for all items of the manuscript: Ideas, statistical applications, formal techniques to analyze data and preparation, creation and presentation of information.

Conflicts of Interest

The author reports no declarations of interest.

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Appendix A

Sexual systems, temporal variation in sexual expression, and spatial separation of sexual organs and functional groups for 144 plant species from xerophytic shrubland in the Venezuelan coastal central zone.

| Plant family Species | Carbon metabolism ^A | Succulence ^B | Life form ^C | Habitat ^D | Dispersal syndrome ^E | Sexuality ^F | Sexuality ^G | Dichogamy ^H | Herkogamy ^I |
|--|---------------------------------|-------------------------|------------------------|----------------------|---------------------------------|------------------------|------------------------|------------------------|------------------------|
| ACANTHACEAE | | | | | | | | | |
| <i>Ruellia tuberosa</i> L. | C ₃ | NS | Ph | D | B-Mi | H | H | AD | H |
| AIZOACEAE | | | | | | | | | |
| <i>Trianthema portulacastrum</i> L. | C ₄ | S | Ah | D | Mi | H | H | AD | NH |
| AMARANTHACEAE | | | | | | | | | |
| <i>Achyranthes aspera</i> L. | C ₃ | NS | Ph | D | E | H | H | AD | NH |
| <i>Alternanthera pungens</i> Kunth | C ₄ | NS | Ph | D | E | H | H | AD | NH |
| <i>Amaranthus crassipes</i> Schlttdl. | C ₄ | NS | Ah | D | G | M | M | PG | NH |
| <i>Amaranthus dubius</i> Mart. ex Thell. | C ₄ | NS | Ah | D | G | M | M | PG | NH |
| <i>Celosia argentea</i> L. | C ₃ ^(2,4) | NS | Ah | D | G | M | M | PG | NH |
| APOCYNACEAE | | | | | | | | | |
| <i>Aspidosperma cuspa</i> (HBK) Blake | C ₃ ⁽⁶⁾ | NS | SH | M | A | H | H | AD | H |
| <i>Calotropis procera</i> (Aiton) W. T. Aiton | C ₃ | S | SH | D | A | H | H | AD | H |
| <i>Marsdenia condensiflora</i> S.F. Blake | C ₃ | NS | L | M | A | H | H | AD | H |
| <i>Plumeria inodora</i> Jacq. | C ₃ | NS | T | M | A | H | H | AD | H |
| <i>Sarcostema clausum</i> (Jacq.) R & Schum | CAM | NS | L | D | A | H | H | AD | H |
| ARACEAE | | | | | | | | | |
| <i>Anthurium ellipticum</i> K. Koch & Bouché | C ₃ | NS | Ph | M | O | H | H | PG | NH |
| ASPARAGACEAE | | | | | | | | | |
| <i>Agave cocui</i> Trel. | CAM | S | Ph | M | A | H | H | PT | H |
| ASTERACEAE | | | | | | | | | |
| <i>Baccharis trinervis</i> Pers | C ₃ | NS | Ph | D | A | gd | D | * | * |
| <i>Condylidium iresinoides</i> (Kunth) R.M. King & H. Rob. | C ₃ | NS | Ah | D | A | H | H | PT | H |

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| | | | | | | | | | |
|---|--------------------------------|----|----|---|-----|----|---|----|----|
| <i>Conyza bonariensis</i> (L.) Cronquist | C ₃ ⁽¹⁰⁾ | NS | Ah | D | A | H | H | PT | NH |
| <i>Eclipta alba</i> (L.) Hassk. | C ₃ ⁽¹⁾ | NS | Ah | D | Mi | H | H | PT | H |
| <i>Launaea intybacea</i> (Jacq.) Beauverd | C ₃ | NS | Ah | D | A | H | H | PT | H |
| <i>Pluchea symphytifolia</i> (Mill.) Giller | C ₃ | NS | SH | D | A | M | M | PT | NH |
| <i>Porophyllum ruderale</i> (Jacq.) Cass. | C ₃ | NS | Ah | D | A | H | H | PG | NH |
| <i>Tessaria integrifolia</i> Ruiz & Pav. | C ₃ | NS | SH | D | A | M | M | PT | H |
| <i>Tridax procumbens</i> L. | C ₃ | NS | Ph | D | A | GM | M | PT | H |
| <i>Wedelia calycina</i> Rich. | C ₃ | NS | Ph | D | Mi | GM | M | PT | NH |
| <i>Wulffia stenoglossa</i> (Cass.) DC. | C ₃ | NS | L | D | O | GM | M | PT | NH |
| BIGNONIACEAE | | | | | | | | | |
| <i>Arrabidaea corallina</i> (Jacq.) Sandwith | C ₃ | NS | L | M | A | H | H | AD | H |
| BORAGINACEAE | | | | | | | | | |
| <i>Bourreria cumanensis</i> (Loefl.) O.E. Schulz | C ₃ | NS | T | M | A | H | H | PT | H |
| <i>Cordia curassavica</i> (Jacq.) Roem. & Schult. | C ₃ | NS | SH | D | O | H | H | AD | H |
| <i>Cordia dentata</i> Poir. | C ₃ | NS | T | D | O-M | H | H | AD | H |
| <i>Cordia globosa</i> (Jacq.) Kunth & Andrews ex A. DC. | C ₃ | NS | SH | D | O | H | H | AD | NH |
| <i>Heliotropium</i> <i>angiospermum</i> Murray | C ₃ | NS | Ah | D | Mi | H | H | AD | NH |
| <i>Heliotropium</i> <i>ternatum</i> Vahl. | C ₄ | NS | Ph | D | Mi | H | H | AD | NH |
| <i>Rochefortia spinosa</i> (Jacq.) Urb. | C ₃ | NS | SH | M | O | d | D | * | * |
| <i>Tournefortia volubilis</i> L. | C ₃ | NS | L | M | O | hh | D | AD | * |
| BROMELIACEAE | | | | | | | | | |
| <i>Tillandsia circinnata</i> Schltdl. | CAM | S | Ph | M | A | H | H | AD | NH |
| <i>Tillandsia flexuosa</i> Sw. | CAM | S | Ph | M | A | H | H | PG | NH |
| <i>Tillandsia recurvata</i> (L.) L. | CAM | S | Ph | D | A | H | H | PT | NH |

Continued

| CACTACEAE | | | | | | | | | |
|--|-------------------------------|----|----|---|-----|---|---|----|----|
| <i>Acanthocereus tetragonus</i> (L.) Hummelinck | CAM ⁽⁷⁾ | S | L | M | O-Q | H | H | AD | H |
| <i>Mammillaria mammillaris</i> (L.) H. Karst. | CAM | S | Ph | M | O-S | H | H | AD | H |
| <i>Melocactus curvispinus</i> ssp. <i>caesius</i> (H.L. Wendl.) N.P. Taylor | CAM | S | Ph | M | O-S | H | H | PT | H |
| <i>Opuntia caracasana</i> Salm-Dyck | CAM | S | Ph | D | O-M | H | H | AD | NH |
| <i>Opuntia elatior</i> Mill. | CAM | S | SH | M | O-M | H | H | AD | H |
| <i>Pereskia guamacho</i> F.A.C. Weber | CAM | S | T | M | O-Q | H | H | PT | H |
| <i>Pilosocereus moritzianus</i> (Otto) Byles & G.D. Rowley | CAM | S | T | M | O-Q | H | H | AD | NH |
| <i>Stenocereus griseus</i> (Haw.) Buxb. | CAM | S | T | M | O-Q | H | H | AD | H |
| CAPPARACEAE | | | | | | | | | |
| <i>Capparis flexuosa</i> (L.) L. | C ₃ | NS | SH | M | O-M | H | H | AD | H |
| <i>Capparis hastata</i> Jacq. | C ₃ | NS | T | M | O | H | H | AD | H |
| <i>Capparis odoratissima</i> Jacq. | C ₃ | NS | SH | M | O | H | H | AD | H |
| <i>Capparis tenuisiliqua</i> Jacq. | C ₃ | NS | SH | M | O | H | H | AD | NH |
| <i>Capparis verrucosa</i> Jacq. | C ₃ | NS | SH | M | O | H | H | AD | H |
| COMMELINACEAE | | | | | | | | | |
| <i>Commelina erecta</i> L. | C ₃ | NS | Ah | D | Mi | H | H | AD | H |
| CONVOLVULACEAE | | | | | | | | | |
| <i>Convolvulus nodiflorus</i> Desr. | C ₃ | NS | L | D | Mi | H | H | AD | H |
| <i>Evolvulus tenuis</i> Mart. ex Choisy ssp. <i>sericatus</i> (House) Ooststr. | C ₃ | NS | Ph | D | G | H | H | AD | H |
| <i>Ipomoea avicola</i> D.F. Austin | C ₃ | NS | L | D | A | H | H | PT | H |
| <i>Ipomoea nil</i> Roth | C ₃ ⁽⁹⁾ | NS | L | D | G | H | H | AD | NH |

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| | | | | | | | | | |
|---|-------------------------------|----|----|---|------|----|---|----|----|
| <i>Jacquemontia cumanensis</i> Kuntze | C ₃ | NS | L | D | G | H | H | AD | NH |
| <i>Merremia umbellata</i> (L.) Hall | C ₃ | NS | L | D | G | H | H | PT | H |
| CUCURBITACEAE | | | | | | | | | |
| <i>Cucumis dipsaceus</i> Ehrenb. | C ₃ | NS | L | D | M | M | M | PG | H |
| EUPHORBIACEAE | | | | | | | | | |
| <i>Acalypha cuspidata</i> Jacq. | C ₃ | NS | Ph | M | B-Mi | M | M | PG | H |
| <i>Chamaesyce berteroaana</i> (Balbis) Millsp | C ₄ ⁽⁸⁾ | NS | Ah | D | G-Mi | M | M | PG | H |
| <i>Chamaesyce hyssopifolia</i> (L.) Small | C ₄ | NS | Ah | D | G-Mi | M | M | PG | H |
| <i>Chamaesyce prostrata</i> (Aiton) Small | C ₄ ⁽⁸⁾ | NS | Ah | D | G-Mi | M | M | PG | H |
| <i>Cnidoscolus urens</i> (L.) Arthur | C ₃ | NS | Ph | M | B-Mi | M | M | PG | H |
| <i>Croton lobatus</i> L. | C ₃ | NS | Ah | D | B-Mi | M | M | PG | H |
| <i>Croton ovalifolius</i> Vahl | C ₃ | NS | Ph | D | B-Mi | M | M | PG | H |
| <i>Euphorbia gollmeriana</i> Klotzsch ex Boiss. | CAM | S | Ph | D | B-Mi | M | M | PT | H |
| <i>Euphorbia heterophylla</i> L. | C ₃ | S | Ah | D | B-Mi | M | M | PT | H |
| <i>Jatropha gossypifolia</i> L. | C ₃ | NS | SH | M | B-Mi | M | M | PT | H |
| <i>Pedilanthus tithymaloides</i> (L.) Poit. | CAM | S | Ph | M | G | M | M | PT | H |
| <i>Ricinus communis</i> L. | C ₃ | NS | SH | D | Mi | M | M | PT | NH |
| FABACEAE | | | | | | | | | |
| <i>Acacia tortuosa</i> (L.) Willd. | C ₃ | NS | T | D | M | AM | M | AD | H |
| <i>Centrosema brasilianum</i> (L.) Benth. | C ₃ | NS | L | D | G | H | H | AD | H |
| <i>Chaetocalyx scandens</i> (L.) Urb. | C ₃ | NS | L | D | E | H | H | AD | H |
| <i>Coursetia caribaea</i> (Jack.) Lavin | C ₃ | NS | Ah | D | G | H | H | AD | H |
| <i>Crotalaria incana</i> L. | C ₃ | NS | Ah | D | B | H | H | AD | H |
| <i>Desmanthus virgatus</i> (L.) Willd. | C ₃ | NS | Ph | D | G | AM | M | AD | NH |

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| | | | | | | | | | |
|---|----------------|----|----|---|-----|----|---|----|----|
| <i>Galactia striata</i> (Jacq.) Urb. | C ₃ | NS | L | D | G | H | H | AD | H |
| <i>Indigofera</i> <i>suffruticosa</i> Mill. | C ₃ | NS | Ph | D | G | H | H | AD | NH |
| <i>Leucaena leucocephala</i> (Lam.) De Wit. | C ₃ | NS | SH | D | G | H | H | AD | H |
| <i>Mimosa arenosa</i> (Willd.) Poir. | C ₃ | NS | T | M | A | AM | M | AD | H |
| <i>Parkinsonia aculeata</i> L. | C ₃ | NS | T | D | A-H | H | H | AD | H |
| <i>Pithecellobium</i> <i>unguis-cati</i> (L.) Benth. | C ₃ | NS | SH | M | O | H | H | AD | H |
| <i>Rhynchosia minima</i> (L.) DC. | C ₃ | NS | Ah | D | O | H | H | AD | NH |
| <i>Senna occidentalis</i> (L.) Link | C ₃ | NS | SH | M | G | H | H | AD | H |
| <i>Stylosanthes hamata</i> (L.) Taubert | C ₃ | NS | Ph | D | E | H | H | AD | H |
| <i>Tephrosia cinerea</i> (L.) Pers. | C ₃ | NS | Ph | D | G | H | H | AD | H |
| MALPIGHIACEAE | | | | | | | | | |
| <i>Heteropterys prunifolia</i> (Kunth) W.R. Anderson | C ₃ | NS | L | D | A | H | H | AD | H |
| <i>Malpighia</i> <i>emarginata</i> DC. | C ₃ | NS | SH | M | O | H | H | AD | H |
| MALVACEAE | | | | | | | | | |
| <i>Abutilon stenopetalum</i> Garcke | C ₃ | NS | SH | D | G | H | H | AD | H |
| <i>Bastardia viscosa</i> (L.) Kunth | C ₃ | NS | Ph | D | G | H | H | AD | H |
| <i>Hibiscus</i> <i>phoeniceus</i> Jacq. | C ₃ | NS | Ph | M | A | H | H | AD | H |
| <i>Malvastrum americanum</i> (L.) Torr. | C ₃ | NS | Ph | D | E | H | H | AD | H |
| <i>Melochia pyramidata</i> var. <i>pyramidata</i> | C ₃ | NS | Ah | D | Mi | H | H | AD | NH |
| <i>Melochia tomentosa</i> L. | C ₃ | NS | Ph | D | Mi | H | H | AD | H |
| <i>Sida ciliaris</i> L. | C ₃ | NS | Ph | D | E | H | H | AD | H |
| <i>Sida spinosa</i> L. | C ₃ | NS | Ah | D | E | H | H | AD | H |
| MUNTINGIACEAE | | | | | | | | | |
| <i>Muntingia calabura</i> L. | C ₃ | NS | T | D | O-Q | H | H | AD | H |

Continued

NYCTAGINACEAE

| | | | | | | | | | |
|--|----------------|----|----|---|----|---|---|----|---|
| <i>Boerhavia diffusa</i> L. | C ₄ | NS | Ah | D | E | H | H | AD | H |
| <i>Boerhavia erecta</i> L. | C ₄ | NS | Ah | D | Mi | H | H | AD | H |
| <i>Guapira pacurero</i> (Kunth) Little. | C ₃ | NS | SH | M | O | d | D | AD | H |

ONAGRACEAE

| | | | | | | | | | |
|---|----------------|----|----|---|---|---|---|----|----|
| <i>Ludwigia octovalvis</i> (Jacq.) Raven | C ₃ | NS | Ah | D | A | H | H | AD | NH |
|---|----------------|----|----|---|---|---|---|----|----|

ORCHIDACEAE

| | | | | | | | | | |
|--|-----|---|----|---|---|---|---|----|---|
| <i>Oncidium cebolleta</i> (Jacq.) Sw. | CAM | S | Ph | M | A | H | H | AD | H |
|--|-----|---|----|---|---|---|---|----|---|

PASSIFLORACEAE

| | | | | | | | | | |
|--|----------------|----|---|---|-------|---|---|----|---|
| <i>Passiflora foetida</i> var. <i>hispida</i> (DC. ex Triana & Planch.) Killip | C ₃ | NS | L | D | O-M-S | H | H | AD | H |
|--|----------------|----|---|---|-------|---|---|----|---|

PHYLLANTHACEAE

| | | | | | | | | | |
|------------------------------|----------------|----|----|---|---|---|---|----|---|
| <i>Phyllanthus niruri</i> L. | C ₃ | NS | Ah | D | G | M | M | PG | H |
|------------------------------|----------------|----|----|---|---|---|---|----|---|

POLYGONACEAE

| | | | | | | | | | |
|----------------------------------|----------------|----|---|---|------|----|---|---|---|
| <i>Coccoloba uvifera</i> (L.) L. | C ₃ | NS | T | D | Ma-H | pd | D | * | * |
|----------------------------------|----------------|----|---|---|------|----|---|---|---|

POACEAE

| | | | | | | | | | |
|---|--------------------------------|----|----|---|------|----|---|----|----|
| <i>Aristida adscensionis</i> L. | C ₄ | NS | Ah | D | E | H | H | AD | H |
| <i>Bothriochloa pertusa</i> (L.) A.Camus | C ₄ | NS | Ah | D | E | H | H | AD | H |
| <i>Cenchrus brownie</i> Roem. & Schult. | C ₄ | NS | Ah | D | E | H | H | PT | H |
| <i>Cenchrus ciliaris</i> L. | C ₄ | NS | Ah | D | E | H | H | PT | H |
| <i>Cenchrus echinatus</i> L. | C ₄ | NS | Ah | D | E | AM | M | PT | H |
| <i>Chloris inflata</i> Link | C ₄ | NS | Ph | D | E | H | H | AD | H |
| <i>Dactyloctenium</i> <i>aegyptium</i> (L.) Richter | C ₄ | NS | Ah | D | E | H | H | AD | H |
| <i>Digitaria insularis</i> (L.) Mez ex Ekman | C ₄ ⁽¹¹⁾ | NS | Ph | D | A | AM | M | PT | H |
| <i>Pappophorum</i> <i>papiferum</i> (Lam.) Kuntze | C ₄ ⁽¹¹⁾ | NS | Ph | M | G | AM | M | PT | H |
| <i>Rhynchelytrum repens</i> (Willd.) C.E. Hubb | C ₄ ⁽¹¹⁾ | NS | Ph | D | A, E | H | H | AD | NH |
| <i>Setaria vulpiseta</i> (Lam.) R.en & Schult | C ₄ | NS | Ph | D | E | AM | M | PG | NH |

Continued

| | | | | | | | | | |
|--|--------------------------------|----|----|---|-----|----|---|----|----|
| <i>Sorghum bicolor</i> (L.) Moench | C ₄ | NS | Ah | D | G | H | H | AD | H |
| <i>Sporobolus pyramidatus</i> (Lam.) Hitchc. | C ₄ ⁽¹¹⁾ | NS | Ph | D | G | H | H | AD | NH |
| <i>Tragus berteronianus</i> schult. | C ₄ | NS | Ah | D | E | H | H | AD | NH |
| <i>Urochloa fusca</i> (Sw.) B.F. Hansen & Wunderlin | C ₄ | NS | Ph | D | O | AM | M | AD | H |
| PORTULACACEAE | | | | | | | | | |
| <i>Portulaca elatior</i> Mart. ex Rohrb. | C ₄ | S | Ph | D | Mi | H | H | AD | H |
| <i>Portulaca halimoides</i> L. | C ₄ ⁽⁵⁾ | S | Ah | D | Mi | H | H | AD | NH |
| <i>Portulaca oleracea</i> L. | C ₄ | S | Ah | D | Mi | H | H | AD | H |
| PRIMULACEAE | | | | | | | | | |
| <i>Jacquinia aristata</i> Jacq. | C ₃ | NS | T | M | O | H | H | PT | H |
| <i>Jacquinia revoluta</i> Jacq. | C ₃ ⁽³⁾ | NS | SH | M | O | H | H | PT | H |
| RUBIACEAE | | | | | | | | | |
| <i>Machaonia ottonis</i> (K. Schum.) Urb. | C ₃ | NS | SH | D | A | H | H | AD | H |
| SANTALACEAE | | | | | | | | | |
| <i>Phoradendron</i> <i>mucronatum</i> (DC.) Krug & Urb. | C ₃ | S | Ph | M | O | u | D | * | * |
| SAPINDACEAE | | | | | | | | | |
| <i>Cardiospermum</i> <i>corindum</i> L. | C ₃ | NS | L | D | A | AM | M | AD | H |
| <i>Urvillea ulmacea</i> Kunth | C ₃ | NS | L | D | A | AM | M | AD | H |
| SAPOTACEAE | | | | | | | | | |
| <i>Bumelia obtusifolia</i> ssp. <i>auxifolia</i> (Roem. & Schult.) Cronquist | C ₃ | NS | SH | M | O-M | H | H | AD | H |
| SCROPHULARIACEAE | | | | | | | | | |
| <i>Capraria biflora</i> L. | C ₃ | NS | Ah | D | A | H | H | AD | H |
| SOLANACEAE | | | | | | | | | |
| <i>Datura innoxia</i> Mill. | C ₃ | NS | Ah | D | Mi | H | H | AD | H |
| <i>Lycianthes</i> sp. | C ₃ | NS | SH | M | O | H | H | AD | H |
| <i>Lycium nodosum</i> Miers | C ₃ | S | SH | M | O | H | H | AD | H |
| <i>Nicotiana glauca</i> Graham | C ₃ | NS | SH | D | A | H | H | AD | H |
| <i>Solanum americanum</i> Miller | C ₃ | NS | Ah | D | O | H | H | AD | H |

Continued

| | | | | | | | | | |
|---|----------------|----|----|---|----|----|---|----|----|
| <i>Solanum gardneri</i> Sendtn. | C ₃ | NS | SH | D | O | AM | M | AD | H |
| TALINACEAE | | | | | | | | | |
| <i>Talinum triangulare</i> (Jacq.) Willd. | CAM | S | Ph | D | Mi | H | H | AD | H |
| VERBENACEAE | | | | | | | | | |
| <i>Lantana canescens</i> Kunth | C ₃ | NS | Ph | D | G | H | H | AD | H |
| <i>Lippia oreganoides</i> Kunth | C ₃ | NS | SH | M | G | H | H | AD | NH |
| <i>Phyla nodiflora</i> var. <i>reptans</i> (Kunth) Moldenke | C ₃ | NS | Ph | D | G | H | H | AD | H |
| VITACEAE | | | | | | | | | |
| <i>Cissus sicyoides</i> L. | CAM | NS | L | D | O | H | H | PT | H |
| ZYGOPHILLACEAE | | | | | | | | | |
| <i>Guaiacum officinale</i> L. | C ₃ | NS | T | M | O | H | H | PT | H |
| <i>Kallstroemia maxima</i> (L.) Hook. & Arn. | C ₄ | NS | Ah | D | G | H | H | PT | H |

^A = References carbon metabolism. 1- Choudhri, G.N. 1993. Soil-plant-water relationships of *Eclipta alba* (Hassk.) in a salt-affected terrestrial ecosystem. In: Towards the rational use of high salinity tolerant plants. 1: 293-305. H. Leigh and A. Al Ma-soom (eds.) Kluwer Academic Publishers. 2- Kadereit, G., T. Borsch, K. Weising & H. Freitag. 2003. Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C₄ photosynthesis. International Journal of Plant Science 164: 959-986. 3- Mooney, H. A., S. H. Bullock and J. R. Ehleringer. 1989. Carbon isotope ratios of plants of a tropical dry forest in Mexico. Functional Ecology 3: 137-142. 4- Muhaidat, R., R. F. Sage and N.G. Dengler. 2007. Diversity of Kranz anatomy and biochemistry in C₄ Eudicots. American Journal of Botany 94: 362-381. 5- Ocampo, G., N.K. Koteyeva, E.V. Vosnesenskaya, G.E. Edwards, T.L. Sage, R.F. Sage and J. T. Columbus. 2013. Evolution of leaf anatomy and photosynthetic pathways in Portulacaceae. American Journal of Botany 100: 2388-2402. 6- Peixoto, M. de M. 2007. Variações sazonais no metabolismo de carbono e relações hídricas em espécies lenhosas do cerrado de diferentes grupos funcionais. Tese (Mestre), Universidade de Brasília, Brazil. 7- Ricalde, M.F., J.L. Andrade, R. Durán, J.M. Dupuy, J.L. Sumá, R. Us-Santamaría and L.S. Santiago. 2010. Environmental regulation of carbon isotope composition and crassulacean acid metabolism in three plant communities along a water availability gradient. Oecologia 164: 871-880. 8- Sage, R.F., M.R. Li & R.K. Monson. 1999. The taxonomic distribution of C₄ photosynthesis. In: sage, R.F., R.K. Monson, eds. C₄ Plant Biology, San Diego, CA USA, Academic Press, 551-584. 9- Silva, L. C. R., M. A. Giorgis, M. Anand, L. Enrico, N. Pérez-Harguindeguy, V. Falczuk, L. L. Tieszen and M. Cabido. 2001. Evidence of shift in C₄ species range in central Argentina during the late holocene. Plant Soil 349: 261-279. 10- Soares, D.J., W. Salles de Oliveira, E.L. Uzuele, S.J. Pinto de Carvalho R.F. Lopez-Ovejero and P. J. Christoffoleti. 2017. Growth and development of *Conyza bonariensis* based on days or thermal units. Pesq. Agropec. Bras., Brasília 52: 45-53. 11- Waller, S.S. & J.K. Lewis. 1979. Occurrence of C₃ and C₄ photosynthetic pathways in North American Grasses. Journal of Range Management 32: 12-28. ^B = Succulence: NS = non-succulent, S = Succulent. ^C = Life form: T = tree, SH = shrub, L = liana, Ph = perennial herb, Ah = annual herb. ^D = Habitat: M = Late seral or undisturbed area, D = disturbed area. ^E = Dispersal syndrome: A = Anemochory, Mi = Mirmecochory, E = Epizoochory, G = Granivorechory, O = Ornithochory, Ma = Mammalochory, Q = Quiropterochory, S = Saurochory, B = Balistic, H = Hydrochory. ^F = Sexuality: H = Hermaphrodite, M = Monoecy (only unisexual flowers), AM = Andromonoecy, GM = Gynomonoecy, D = Dioecy: gd = gynodioecious, d = dioecious morphologically heterostylous, hh = dioecious morphologically heteromorphic, u = dioecious with unisexual flowers, pd = polygamous dioecious (see Madriz and Ramírez 1997): Madriz, R. & N. Ramírez. 1997. Biología Reproductiva de *Coccoloba uvifera* (L.) Jacq. (Polygonaceae), una especie polígamo-dioica. Revista de Biología Tropical 44/45: 105-115. ^G = Sexuality: H = Hermaphrodite, M = Monoecy, D = dioecy. ^H = Temporal variation in sexual expression: AD = Adichogamy, PT = Protandry, PG = Protogyny. ^I = Variation spatial of sexual organs: H = Herkogamy, NH = No Herkogamy. * = Data no determined or unavailable.

Appendix B

Results of experimental tests for 62 plant species from a xerophytic shrubland from the Venezuelan Central Coastal Region.

| FAMILY | Ovule/flower | Experimental test | | | | | | | | | | | |
|----------------------------------|--------------|---|------|------|----------|-----------|-----|-----|-----|----------|------|------|------|
| | | Number of flowers under experimental test | | | | Fruit set | | | | Seed set | | | |
| Species | ξ | E | SSP | SP | CP | E | SSP | SP | CP | E | SSP | SP | CP |
| AMARANTHACEAE | | | | | | | | | | | | | |
| <i>Achyranthes aspera</i> | 1.00 | 43 | 136 | 91 | 42 | 0 | 119 | 79 | 41 | 0 | 119 | 79 | 41 |
| <i>Alternanthera pungens</i> | 1.00 | 50 | 304 | 44 | 27 | 0 | 3 | 2 | 1 | 0 | 3 | 2 | 1 |
| APOCYNACEAE | | | | | | | | | | | | | |
| <i>Plumeria inodora</i> | 134.84 | 50 | 50 | 24 | 37 | 0 | 0 | 5 | 25 | 0 | 0 | 372 | 1850 |
| ARACEAE | | | | | | | | | | | | | |
| <i>Anthurium ellipticum</i> | 1.61 | 156 | 3423 | 2541 | 3157 | 0 | 0 | 220 | 592 | 0 | 0 | 289 | 998 |
| ASTERACEAE | | | | | | | | | | | | | |
| <i>Condylium iresinoides</i> | 1.00 | 63 | 190 | 30 | 96 | 0 | 21 | 7 | 28 | 0 | 21 | 7 | 28 |
| <i>Launaea intybacea</i> | 1.00 | 328 | 892 | 936 | 587 | 0 | 417 | 853 | 561 | 0 | 417 | 853 | 561 |
| <i>Porophyllum ruderales</i> | 1.00 | 1425 | 1710 | 456 | 399 | 194 | 532 | 247 | 242 | 194 | 532 | 247 | 242 |
| <i>Tessaria integrifolia</i> | 1.00 | NA | 6333 | NA | 1015 | NA | 183 | NA | 61 | NA | 183 | NA | 61 |
| <i>Tridax procumbens</i> | 1.00 | 116 | 174 | 174 | 151 | 0 | 11 | 59 | 83 | 0 | 11 | 59 | 83 |
| BORAGINACEAE | | | | | | | | | | | | | |
| <i>Cordia curassavica</i> (B) | 4.04 | 13 | 498 | 28 | 16 (bxb) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Heliotropium angiospermum</i> | 4.76 | 24 | 80 | 24 | 48 | 1 | 50 | 10 | 35 | 2 | 111 | 29 | 125 |
| <i>Heliotropium ternatum</i> | 3.95 | 25 | 76 | 30 | 61 | 0 | 0 | 0 | 36 | 0 | 0 | 0 | 121 |
| BROMELIACEAE | | | | | | | | | | | | | |
| <i>Tillandsia circinnata</i> | 137.27 | 30 | 57 | 16 | 34 | 0 | 15 | 5 | 14 | 0 | 1271 | 598 | 1295 |
| <i>Tillandsia flexuosa</i> | 197.01 | 31 | 99 | 32 | 27 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 1611 |
| CACTACEAE | | | | | | | | | | | | | |
| <i>Mammillaria mammillaris</i> | 72.61 | 12 | 28 | 26 | 11 | 2 | 12 | 13 | 7 | 105 | 1043 | 1010 | 706 |
| <i>Pereskia guamacho</i> | 17.70 | 20 | 45 | 12 | NA | 0 | 0 | 0 | NA | 0 | 0 | 0 | NA |
| CAPPARACEAE | | | | | | | | | | | | | |
| <i>Capparis odoratissima</i> | 29.09 | NA | 220 | 29 | 7 | NA | 3 | 3 | 5 | NA | 3 | 8 | 22 |
| <i>Capparis tenuisiliqua</i> | 32.67 | 30 | 259 | 18 | 15 | 0 | 9 | 2 | 7 | 0 | 9 | 2 | 36 |

Continued

CONVOLVULACEAE

| | | | | | | | | | | | | | |
|---|------|----|-----|----|----|---|---|---|----|---|---|----|----|
| <i>Evolvulus tenuis</i> ssp. <i>sericatus</i> | 3.57 | 19 | 185 | 55 | 54 | 0 | 0 | 3 | 30 | 0 | 0 | 11 | 87 |
| <i>Jacquemontia cumanensis</i> | 3.98 | 15 | 126 | 21 | 46 | 0 | 4 | 0 | 37 | 0 | 4 | 0 | 51 |

CUCURBITACEAE

| | | | | | | | | | | | | | |
|--------------------------|--------|----|----|----|----|---|---|----|---|---|---|-----|------|
| <i>Cucumis dipsaceus</i> | 434.67 | 20 | 30 | 30 | 55 | 0 | 0 | 10 | 3 | 0 | 0 | 940 | 4080 |
|--------------------------|--------|----|----|----|----|---|---|----|---|---|---|-----|------|

EUPHORBIACEAE

| | | | | | | | | | | | | | |
|----------------------------------|------|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Acalypha cuspidata</i> | 2.75 | 40 | 56 | 29 | 65 | 2 | 16 | 4 | 13 | 0 | 32 | 8 | 32 |
| <i>Croton lobatus</i> | 2.96 | 35 | 57 | 41 | 42 | 2 | 36 | 25 | 23 | 4 | 88 | 75 | 58 |
| <i>Croton ovalifolius</i> | 3.00 | 34 | 63 | 22 | 26 | 0 | 0 | 12 | 19 | 0 | 0 | 25 | 41 |
| <i>Euphorbia gollmeriana</i> | 3.00 | 23 | 97 | 27 | 30 | 0 | 15 | 12 | 24 | 0 | 31 | 28 | 64 |
| <i>Jatropha gossypifolia</i> | 3.00 | 12 | 32 | 20 | 53 | 0 | 2 | 7 | 23 | 0 | 3 | 21 | 58 |
| <i>Pedilanthus tithymaloides</i> | 3.00 | 15 | 66 | 34 | 37 | 0 | 4 | 2 | 3 | 0 | 10 | 2 | 7 |
| <i>Ricinus communis</i> | 3.00 | 56 | 76 | 78 | 9 | 39 | 27 | 22 | 9 | 99 | 64 | 38 | 27 |

FABACEAE

| | | | | | | | | | | | | | |
|--------------------------------|-------|------|------|------|------|---|----|----|----|----|-----|-----|------|
| <i>Acacia tortuosa</i> | 11.27 | 1000 | 1440 | 120 | 300 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 7 |
| <i>Centrosema brasilianum</i> | 19.90 | 13 | 44 | 29 | 15 | 0 | 9 | 16 | 6 | 0 | 152 | 217 | 82 |
| <i>Chaetocalyx scandens</i> | 11.66 | 16 | 168 | 18 | 31 | 0 | 0 | 12 | 22 | 0 | 0 | 60 | 132 |
| <i>Coursetia caribaea</i> | 22.47 | 14 | 101 | 24 | 30 | 0 | 32 | 13 | 25 | 0 | 482 | 238 | 480 |
| <i>Crotalaria incana</i> | 30.27 | 30 | 169 | 27 | 38 | 2 | 30 | 16 | 18 | 34 | 689 | 217 | 358 |
| <i>Desmanthus virgatus</i> | 20.78 | 37 | 84 | 43 | 52 | 0 | 65 | 24 | 36 | 0 | 919 | 310 | 493 |
| <i>Indigofera suffruticosa</i> | 5.29 | 130 | 31 | 23 | 15 | 0 | 0 | 1 | 3 | 0 | 0 | 4 | 15 |
| <i>Mimosa arenosa</i> | 7.25 | 100 | 3620 | 1991 | 2172 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 5 |
| <i>Rhynchosia minima</i> | 2.0 | 26 | 81 | 39 | 25 | 1 | 45 | 22 | 15 | 0 | 72 | 32 | 25 |
| <i>Senna occidentalis</i> | 55.97 | 19 | 59 | 28 | 36 | 0 | 2 | 25 | 36 | 0 | 10 | 827 | 1180 |
| <i>Tephrosia cinerea</i> | 10.51 | 26 | 155 | 46 | 48 | 0 | 47 | 24 | 25 | 0 | 436 | 221 | 234 |

MALPIGHIACEAE

| | | | | | | | | | | | | | |
|--------------------------------|------|----|-----|----|----|---|---|---|----|---|---|---|----|
| <i>Heteropterys prunifolia</i> | 3.00 | 56 | 152 | 10 | 50 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 60 |
|--------------------------------|------|----|-----|----|----|---|---|---|----|---|---|---|----|

MALVACEAE

| | | | | | | | | | | | | | |
|------------------------------|-------|----|----|----|----|---|----|----|----|----|------|-----|-----|
| <i>Bastardia viscosa</i> | 6.60 | 18 | 27 | 21 | 23 | 0 | 17 | 10 | 17 | 0 | 62 | 51 | 84 |
| <i>Hibiscus phoeniceus</i> | 26.69 | 17 | 53 | 26 | 70 | 0 | 36 | 22 | 48 | 0 | 626 | 469 | 931 |
| <i>Malvastrum americanum</i> | 12.53 | 29 | 93 | 34 | 21 | 3 | 83 | 28 | 17 | 28 | 1047 | 326 | 199 |
| <i>Sida ciliaris</i> | 7.09 | 22 | 48 | 33 | 29 | 0 | 37 | 29 | 28 | 0 | 191 | 149 | 148 |

Continued

| | | | | | | | | | | | | | |
|---|---------|-----|-----|-----|-----|----|-----|----|----|-----|------|--------|--------|
| <i>Sida spinosa</i> | 4.98 | 16 | 83 | 25 | 31 | 0 | 51 | 23 | 32 | 0 | 242 | 101 | 151 |
| MUNTINGIACEAE | | | | | | | | | | | | | |
| <i>Muntingia calabura</i> | 3294.69 | 20 | 56 | 12 | 20 | 0 | 5 | 3 | 4 | 0 | 1221 | 6121 | 8813 |
| NYCTAGINACEAE | | | | | | | | | | | | | |
| <i>Boerhavia diffusa</i> | 1.00 | 64 | 762 | 35 | 19 | 0 | 591 | 32 | 18 | 0 | 582 | 32 | 18 |
| ONAGRACEAE | | | | | | | | | | | | | |
| <i>Ludwigia octovalis</i> | 1673.81 | 36 | 68 | 28 | 31 | 1 | 36 | 19 | 27 | 427 | 8807 | 17,603 | 26,690 |
| PASSIFLORACEAE | | | | | | | | | | | | | |
| <i>Passiflora foetida</i> var. <i>hispida</i> | 57.24 | 14 | 25 | 19 | 15 | 0 | 17 | 13 | 9 | 0 | 353 | 290 | 261 |
| PHYLLANTHACEAE | | | | | | | | | | | | | |
| <i>Phyllanthus niruri</i> | 6.00 | 100 | 128 | 34 | 66 | 52 | 90 | 19 | 39 | 308 | 532 | 119 | 227 |
| POACEAE | | | | | | | | | | | | | |
| <i>Cenchrus ciliaris</i> | 1.00 | 43 | 367 | 137 | 122 | 0 | 143 | 37 | 71 | 0 | 143 | 37 | 71 |
| <i>Tragus berteronianus</i> | 1.00 | 21 | 148 | 204 | 136 | 0 | 106 | 94 | 70 | 0 | 105 | 92 | 67 |
| PORTULACACEAE | | | | | | | | | | | | | |
| <i>Portulaca elatior</i> | 203.55 | 19 | 51 | 38 | 27 | 1 | 46 | 32 | 25 | 5 | 6457 | 3911 | 2159 |
| <i>Portulaca oleracea</i> | 95.81 | 26 | 39 | 28 | 61 | 0 | 37 | 22 | 56 | 0 | 1802 | 1865 | 4184 |
| SCROPHULARIACEAE | | | | | | | | | | | | | |
| <i>Capraria biflora</i> | 518.26 | 10 | 61 | 18 | 23 | 0 | 43 | 18 | 23 | 0 | 6897 | 5358 | 7210 |
| SOLANACEAE | | | | | | | | | | | | | |
| <i>Datura innoxia</i> | 420.25 | 21 | 21 | 25 | 12 | 0 | 15 | 20 | 12 | 0 | 3512 | 5800 | 3481 |
| <i>Lycium nodosum</i> | 30.08 | 20 | 31 | 40 | 40 | 0 | 3 | 10 | 20 | 0 | 1 | 10 | 90 |
| <i>Solanum americanum</i> | 69.98 | 29 | 71 | 29 | 32 | 1 | 27 | 20 | 27 | 51 | 785 | 509 | 1141 |
| TALINACEAE | | | | | | | | | | | | | |
| <i>Talinum triangulare</i> | 76.12 | 20 | 120 | 41 | 52 | 1 | 33 | 26 | 41 | 0 | 1541 | 1195 | 1889 |
| VERBENACEAE | | | | | | | | | | | | | |
| <i>Lantana canescens</i> | 2.00 | 91 | 359 | 63 | 130 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 59 |
| <i>Phyla nodiflora</i> var. <i>reptans</i> | 2.00 | 34 | 112 | 43 | 64 | 1 | 29 | 15 | 23 | 0 | 58 | 32 | 45 |
| ZYGOPHILLACEAE | | | | | | | | | | | | | |
| <i>Guaiaicum officinale</i> | 16.36 | 10 | 34 | 6 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |

(B) = short style individual of distylous species. E = Emasculation; SSP = Spontaneous self-pollination; SP = Hand self-pollination; CP = Cross-pollinations; NA = Test was not performed.

Supplemental Material

Supplementary Material 1. Agamospermy indexes and their qualitative categories for 66 plant species.

| FAMILY | Agamospermy index [AGI (sp)] | | | | Agamospermy index [AGI (cp)] | | | | Conclusion AGI ¹ |
|--|------------------------------|----------|------------|----------|------------------------------|----------|------------|----------|--------------------------------|
| | Fruit level | | Seed level | | Fruit level | | Seed level | | |
| Species (B or L) | Index | Category | Index | Category | Index | Category | Index | Category | |
| AMARANTHACEAE | | | | | | | | | |
| <i>Achyranthes aspera</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Alternanthera pungens</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| APOCYNACEAE | | | | | | | | | |
| <i>Plumeria inodora</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| ARACEAE | | | | | | | | | |
| <i>Anthurium ellipticum</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| ASTERACEAE | | | | | | | | | |
| <i>Condylium iresinoides</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Launaea intybacea</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Porophyllum ruderales</i> | 0.2513 | PAG (sp) | 0.2513 | PAG (sp) | 0.2245 | PAG (cp) | 0.2245 | PAG (cp) | PAG |
| <i>Tridax procumbens</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| BORAGINACEAE | | | | | | | | | |
| <i>Cordia curassavica</i> (B) | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | | | | | NAG |
| <i>Heliotropium angiospermum</i> | 0.1000 | NAG (sp) | 0.0690 | NAG (sp) | 0.0571 | NAG (cp) | 0.0320 | NAG (cp) | NAG |
| <i>Heliotropium ternatum</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Tournefortia volubilis</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| BROMELIACEAE | | | | | | | | | |
| <i>Tillandsia circinnata</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Tillandsia flexuosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| CACTACEAE | | | | | | | | | |
| <i>Mammillaria mammillaris</i> | 0.3333 | PAG (sp) | 0.2252 | PAG (sp) | 0.2619 | NAG (cp) | 0.1363 | PAG (cp) | PAG |
| <i>Melocactus curvispinus</i> ssp. <i>caesius</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Pereskia guamacho</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | | | | | NAG |
| <i>Pilosocereus moritzianus</i> | 0.0000 | NAG (sp) | | | 0.0000 | NAG (cp) | | | NAG |
| <i>Stenocereus griseus</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| CAPPARACEAE | | | | | | | | | |
| <i>Capparis tenuisiliqua</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |

Continued

CONVOLVULACEAE

| | | | | | | | | | |
|--------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Evolvulus tenuis</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Jacquemontia cumanensis</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |

CUCURBITACEAE

| | | | | | | | | | |
|--------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Cucumis dipsaceus</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
|--------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|

EUPHORBIACEAE

| | | | | | | | | | |
|----------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Acalypha cuspidata</i> | 0.3625 | PAG (sp) | 0.0000 | NAG (sp) | 0.0000 | PAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Croton lobatus</i> | 0.0937 | NAG (sp) | 0.0625 | PAG (sp) | 0.1043 | NAG (cp) | 0.0828 | PAG (cp) | NAG |
| <i>Croton ovalifolius</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Euphorbia gollmeriana</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Jatropha gossypifolia</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Pedilanthus tithymaloides</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Ricinus communis</i> | 2.4058 | PAS (sp) | 3.6288 | PAS (sp) | 0.0000 | PAG (cp) | 0.5893 | PAG (cp) | PAG |

FABACEAE

| | | | | | | | | | |
|--------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Acacia tortuosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Centrosema brasilianum</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Chaetocalyx scandens</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Coursetia caribaea</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Crotalaria incana</i> | 0.1125 | NAG (sp) | 0.1410 | PAG (sp) | 0.0000 | PAG (cp) | 0.1203 | PAG (cp) | PAG |
| <i>Desmanthus virgatus</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Indigofera suffruticosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Mimosa arenosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Rhynchosia minima</i> | 0.0682 | NAG (sp) | 0.0469 | NAG (sp) | 0.0000 | NAG (cp) | 0.0385 | NAG (cp) | NAG |
| <i>Senna occidentalis</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Tephrosia cinerea</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |

MALPIGHIACEAE

| | | | | | | | | | |
|--------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Heteropterys prunifolia</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
|--------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|

MALVACEAE

| | | | | | | | | | |
|-------------------------------|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| <i>Bastardia viscosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Hibiscus phoeniceus</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Malvastrum americanum</i> | 0.1256 | PAG (sp) | 0.1007 | PAG (sp) | 0.1278 | NAG (cp) | 0.1019 | PAG (cp) | PAG |
| <i>Melochia tomentosa</i> (L) | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Melochia tomentosa</i> (B) | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Sida ciliaris</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Sida spinosa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |

Continued

| | | | | | | | | | |
|---|--------|----------|--------|----------|--------|----------|--------|----------|-----|
| MUNTINGIACEAE | | | | | | | | | |
| <i>Muntingia calabura</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| NYCTAGINACEAE | | | | | | | | | |
| <i>Boerhavia diffusa</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| ONAGRACEAE | | | | | | | | | |
| <i>Ludwigia octovalvis</i> | 0.0409 | NAG (sp) | 0.0189 | PAG (sp) | 0.037 | NAG (cp) | 0.0138 | PAG (cp) | NAG |
| PASSIFLORACEAE | | | | | | | | | |
| <i>Passiflora foetida</i> var. <i>hispidula</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| PHYLLANTHACEAE | | | | | | | | | |
| <i>Phyllanthus niruri</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| POACEAE | | | | | | | | | |
| <i>Cenchrus ciliaris</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Tragus berteronianus</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| POLYGONACEAE | | | | | | | | | |
| <i>Coccoloba uvifera</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| PORTULACACEAE | | | | | | | | | |
| <i>Portulaca elatior</i> | 0.0625 | NAG (sp) | 0.0026 | NAG (sp) | 0.0568 | NAG (cp) | 0.0033 | NAG (cp) | NAG |
| <i>Portulaca oleracea</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| SCROPHULARIACEAE | | | | | | | | | |
| <i>Capraria biflora</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| SOLANACEAE | | | | | | | | | |
| <i>Datura innoxia</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Lycium nodosum</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Solanum americanum</i> | 0.0500 | NAG (sp) | 0.1002 | PAG (sp) | 0.0409 | NAG (cp) | 0.0493 | PAG (cp) | NAG |
| TALINACEAE | | | | | | | | | |
| <i>Talinum triangulare</i> | 0.0788 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| VERBENACEAE | | | | | | | | | |
| <i>Lantana canescens</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |
| <i>Phyla nodiflora</i> var. <i>reptans</i> | 0.0843 | NAG (sp) | 0.0790 | NAG (sp) | 0.0818 | NAG (cp) | 0.0837 | PAG (cp) | NAG |
| ZYGOPHILLACEAE | | | | | | | | | |
| <i>Guaicum officinale</i> | 0.0000 | NAG (sp) | 0.0000 | NAG (sp) | 0.0000 | NAG (cp) | 0.0000 | NAG (cp) | NAG |

[AGI (sp)] = Agamospermy index determined as dividing the results obtained from the agamospermy test by the results obtained from the self-pollination test. [AGI (cp)] = Agamospermy index determined as dividing the results obtained from the agamospermy test by the results obtained from the cross-pollination. ¹ = NAG (No agamospermy); PAG (Partial agamospermy); PCSM (Partial constrained sexual mating). B = brevi style individuals, L= Longi style individuals.

Supplementary Material 2. Breeding system indexes and their qualitative categories for 74 plant species.

| FAMILY | Spontaneous self-pollination index (SSPI) | | | | Conclusion SSPI ¹ | Self-fertility index (SFI) | | | | Conclusion SFI ² | Self-incompatibility index (ISI) | | | | Conclusion ISI ³ | Composite Breeding System ⁴ |
|--------------------------------|---|----------|------------|----------|------------------------------|----------------------------|----------|------------|----------|-----------------------------|----------------------------------|----------|------------|----------|-----------------------------|--|
| | Fruit level | | Seed level | | | Fruit level | | Seed level | | | Fruit level | | Seed level | | | |
| | Index | Category | Index | Category | | Index | Category | Index | Category | | Index | Category | Index | Category | | |
| AMARANTHACEAE | | | | | | | | | | | | | | | | |
| <i>Achyranthes aspera</i> | 1.0079 | PCASP | 1.0079 | PCASP | PCASP | 0.8963 | PX | 0.8963 | PX | PX | 0.8893 | PSI | 0.8893 | PSI | PSI | NAG, POSP, PX, PSI |
| <i>Alternanthera pungens</i> | 0.2171 | PSSP | 0.2171 | PSSP | PSSP | 0.2664 | PX | 0.2664 | PX | PX | 1.2273 | SC | 1.2273 | SC | SC | NAG, PSSP, PX, SC |
| APOCYNACEAE | | | | | | | | | | | | | | | | |
| <i>Calotropis procera</i> | | | | | NSSP ¹ | | | | | X ¹ | | | | | | |
| <i>Marsdenia condensiflora</i> | | | | | NSSP ¹ | | | | | X ¹ | | | | | | |
| <i>Plumeria inodora</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.2833 | PSI | 0.2849 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Sarcostema clausum</i> | | | | | NSSP ¹ | | | | | X ¹ | | | | | | |
| ARACEAE | | | | | | | | | | | | | | | | |
| <i>Anthurium ellipticum</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.4617 | PSI | 0.3598 | PSI | PSI | NAG, NSSP, X, PSI |
| ASTERACEAE | | | | | | | | | | | | | | | | |
| <i>Condylium iresinoides</i> | 0.4737 | PSSP | 0.4737 | PSSP | PSSP | 0.1965 | PX | 0.1965 | PX | PX | 0.4148 | PSI | 0.4148 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Launaea intybacea</i> | 0.513 | PSSP | 0.513 | PSSP | PSSP | 0.4892 | PX | 0.4892 | PX | PX | 0.9536 | PSI | 0.9536 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Porophyllum ruderale</i> | 0.5744 | PSSP | 0.5744 | PSSP | PSSP | 0.5129 | PX | 0.5129 | PX | PX | 0.8931 | PSI | 0.8931 | PSI | PSI | PAG, PSSP, PX, PSI |
| <i>Tessaria integrifolia</i> | | | | | | 0.4977 | PX | 0.4977 | PX | PX | | | | | | PX |
| <i>Tridax procumbens</i> | 0.1864 | PSSP | 0.1864 | PSSP | PSSP | 0.115 | PX | 0.115 | PX | PX | 0.6169 | PSI | 0.6169 | PSI | PSI | NAG, PSSP, PX, PSI |
| BORAGINACEAE | | | | | | | | | | | | | | | | |
| <i>Cordia curassavica</i> (B) | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | | | | | | | | | | | NAG, NSSP |

Continued

| | | | | | | | | | | | | | | | | |
|--|--------|-------|--------|-------|-------|--------|----|--------|----|----|--------|-----|--------|-----|-----|--------------------------|
| <i>Heliotropium angiospermum</i> | 1.5000 | PCASP | 1.1483 | PCASP | PCASP | 0.8571 | PX | 0.5328 | PX | PX | 0.5714 | PSI | 0.4640 | PSI | PSI | NAG, POSP, PX, PSI |
| <i>Heliotropium ternatum</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| <i>Tournefortia volubilis</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| BROMELIACEAE | | | | | | | | | | | | | | | | |
| <i>Tillandsia circinnata</i> | 0.8421 | PSSP | 0.5966 | PSSP | PSSP | 0.6391 | PX | 0.5854 | PX | PX | 0.7589 | PSI | 0.9813 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Tillandsia flexuosa</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| CACTACEAE | | | | | | | | | | | | | | | | |
| <i>Mammillaria mammillaris</i> | 0.8571 | PSSP | 0.9589 | PSSP | PSSP | 0.6735 | PX | 0.5804 | PX | PX | 0.7857 | PSI | 0.6053 | PSI | PSI | PAG, PSSP, PX, PSI |
| <i>Melocactus curvispinus ssp. caesius</i> | 0.8966 | PSSP | 0.8448 | PSSP | PSSP | 0.7754 | PX | 0.7851 | PX | PX | 0.8649 | PSI | 0.9294 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Pereskia guamacho</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | | | | | | | | | | | NAG, NSSP |
| <i>Pilosocereus moritzianus</i> | 0.0000 | NSSP | | | NSSP | 0.0000 | X | | | X | 0.3611 | PSI | | | PSI | NAG, NSSP, X, PSI |
| <i>Stenocereus griseus</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | | | X | 0.0000 | SI | | | SI | NAG, NSSP, X, SI |
| CAPPARACEAE | | | | | | | | | | | | | | | | |
| <i>Capparis odoratissima</i> | 0.1318 | PSSP | 0.0494 | PSSP | PSSP | 0.0191 | X | 0.0043 | X | X | 0.1448 | PSI | 0.0878 | PSI | PSI | PSSP, X, PSI |
| <i>Capparis tenuisiliqua</i> | 0.3127 | PSSP | 0.3127 | PSSP | PSSP | 0.0745 | PX | 0.0145 | PX | PX | 0.2381 | PSI | 0.0463 | PSI | PSI | NAG, PSSP, PX, PSI |
| CONVOLVULACEAE | | | | | | | | | | | | | | | | |
| <i>Evolvulus tenuis</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0982 | PSI | 0.1241 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Jacquemontia cumanensis</i> | ∞ | OSSP | ∞ | OSSP | OSSP | 0.0395 | X | 0.0286 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, OSP, X, SI |
| CUCURBITACEAE | | | | | | | | | | | | | | | | |
| <i>Cucumis dipsaceus</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.5556 | PSI | 0.3840 | PSI | PSI | NAG, NSSP, X, PSI |

Continued

EUPHORBIACEAE

| | | | | | | | | | | | | | | | | |
|----------------------------------|--------|-------|--------|-------|-------------------|--------|----|--------|----|----------------|--------|-----|--------|-----|-----|--------------------------|
| <i>Acalypha cuspidata</i> | 2.0714 | PCASP | 2.0714 | PCASP | PCASP | 1.4286 | PE | 1.1607 | PE | PE | 0.6897 | PSI | 0.5603 | PSI | PSI | NAG, POSP, PE, PSI |
| <i>Cnidocolus urens</i> | | | | | NSSP ² | | | | | X ² | | | | | | |
| <i>Croton lobatus</i> | 1.0358 | PCASP | 0.8440 | PSSP | PSSP | 1.1533 | PE | 1.1180 | PE | PE | 1.1135 | PCI | 1.3246 | PCI | PCI | NAG, PSSP, PE, PCI |
| <i>Croton ovalifolius</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.7464 | PSI | 0.7206 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Euphorbia gollmeriana</i> | 0.3479 | PSSP | 0.3082 | PSSP | PSSP | 0.1933 | PX | 0.1498 | PX | PX | 0.5556 | PSI | 0.4861 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Jatropha gossypifolia</i> | 0.1786 | PSSP | 0.0893 | PSSP | PSSP | 0.1440 | PX | 0.0857 | PX | PX | 0.8065 | PSI | 0.9595 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Pedilanthus tithymaloides</i> | 1.0303 | SSP | 2.5758 | PCASP | PCASP | 0.7475 | PX | 0.8009 | PX | PX | 0.7255 | PSI | 0.3109 | PSI | PSI | NAG, POSP, PX, PSI |
| <i>Ricinus communis</i> | 1.2596 | PCASP | 1.7285 | PCASP | PCASP | 0.3553 | PX | 0.2807 | PX | PX | 0.2821 | PSI | 0.1624 | PSI | PSI | PAG, POSP, PX, PSI |

FABACEAE

| | | | | | | | | | | | | | | | | |
|--------------------------------|--------|-------|--------|-------|-------|--------|----|--------|----|----|--------|-----|--------|-----|-----|--------------------------|
| <i>Acacia tortuosa</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| <i>Centrosema brasilianum</i> | 0.3707 | PSSP | 0.4617 | PSSP | PSSP | 0.5114 | PX | 0.6319 | PX | PX | 1.3793 | PCI | 1.3688 | PCI | PCI | NAG, PSSP, PX, PCI |
| <i>Chaetocalyx scandens</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.9394 | PSI | 0.7828 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Coursetia caribaea</i> | 0.5849 | PSSP | 0.4812 | PSSP | PSSP | 0.3802 | PX | 0.2983 | PX | PX | 0.6500 | PSI | 0.6198 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Crotalaria incana</i> | 0.2996 | PSSP | 0.5073 | PSSP | PSSP | 0.3748 | PX | 0.4327 | PX | PX | 1.2510 | PCI | 0.8531 | PSI | PSI | PAG, PSSP, PX, PSI |
| <i>Desmanthus virgatus</i> | 1.3864 | PCASP | 1.5175 | PCASP | PCASP | 1.1177 | PE | 1.1540 | PE | PE | 0.8062 | PSI | 0.7604 | PSI | PSI | NAG, POSP, PE, PSI |
| <i>Indigofera suffruticosa</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.2174 | | 0.1739 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Mimosa arenosa</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |

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|---|--------|-------|--------|-------|-------|--------|----|--------|----|----|--------|-----|--------|-----|-----|--------------------------|
| <i>Rhynchosia minima</i> | 0.9848 | SSP | 1.0833 | PCASP | SSP | 0.9259 | PX | 0.8889 | PX | PX | 0.9402 | PSI | 0.8205 | PSI | PSI | NAG, SSP, PX, PSI |
| <i>Senna occidentalis</i> | 0.0380 | NSSP | 0.0057 | NSSP | NSSP | 0.0339 | X | 0.0052 | X | X | 0.8929 | PSI | 0.9011 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Tephrosia cinerea</i> | 0.5822 | PSSP | 0.5770 | PSSP | PSSP | 0.5812 | PX | 0.5855 | PX | PX | 0.9983 | SC | 1.0147 | PCI | SC | NAG, PSSP, PX, SC |
| MALPIGHIACEAE | | | | | | | | | | | | | | | | |
| <i>Heteropterys prunifolia</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| MALVACEAE | | | | | | | | | | | | | | | | |
| <i>Bastardia viscosa</i> | 1.3222 | PCASP | 0.9455 | PSSP | PSSP | 0.8519 | PX | 0.6287 | PX | PX | 0.6443 | PSI | 0.6650 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Hibiscus phoeniceus</i> | 0.8027 | PSSP | 0.6548 | PSSP | PSSP | 0.9906 | A | 0.8881 | PX | PX | 1.2340 | PCI | 1.3563 | PCI | PCI | NAG, PSSP, PX, PCI |
| <i>Malvastrum americanum</i> | 1.0837 | PCASP | 1.1742 | PCASP | PCASP | 1.1025 | PE | 1.1880 | PE | PE | 1.0173 | SC | 1.0118 | PCI | SC | PAG, POSP, PE, SC |
| <i>Melochia pyramidata</i> <i>var.pyramidata</i> | 0.8619 | PSSP | 1.0368 | PCASP | PSSP | | | | | | | | | | | PSSP |
| <i>Melochia tomentosa</i> (L) | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0991 | SI | 0.0153 | SI | SI | NAG, NSSP, X, SI |
| <i>Melochia tomentosa</i> (B) | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.1617 | PSI | 0.0486 | PSI | PSI | NAG, NSSP, X, PSI |
| <i>Sida ciliaris</i> | 0.8772 | PSSP | 0.8813 | PSSP | PSSP | 0.7984 | PX | 0.7797 | PX | PX | 0.9102 | PSI | 0.8847 | PSI | PSI | NAG, PSSP, PX, PSI |
| <i>Sida spinosa</i> | 0.6679 | PSSP | 0.7217 | PSSP | PSSP | 0.6343 | PX | 0.6179 | PX | PX | 0.9497 | PSI | 0.8562 | PSI | PSI | NAG, PSSP, PX, PSI |
| MUNTINGIACEAE | | | | | | | | | | | | | | | | |
| <i>Muntingia calabura</i> | 0.3571 | PSSP | 0.0427 | PSSP | PSSP | 0.4464 | PX | 0.0495 | PX | PX | 1.2500 | PCI | 1.1576 | PCI | PCI | NAG, PSSP, PX, PCI |
| NYCTAGINACEAE | | | | | | | | | | | | | | | | |
| <i>Boerhavia diffusa</i> | 0.8483 | PSSP | 0.8354 | PSSP | PSSP | 0.8187 | PX | 0.8062 | PX | PX | 0.9651 | PSI | 0.9651 | PSI | PSI | NAG, PSSP, PX, PSI |
| ONAGRACEAE | | | | | | | | | | | | | | | | |
| <i>Ludwigia octovalvis</i> | 1.8947 | PCASP | 0.2060 | PSSP | PSSP | 1.3333 | PE | 0.1504 | PX | PX | 0.7037 | PSI | 0.7302 | PSI | PSI | NAG, PSSP, PX, PSI |

Continued

ORCHIDACEAE

Oncidium cebolleta NSSP¹ X¹

PASSIFLORACEAE

Passiflora foetida 0.9938 SSP 0.9251 PSSP PSSP 1.1333 PE 0.8115 PX PX 1.1404 PCI 0.8772 PSI PSI NAG,
var. *hispida* PSSP PX, PSI

PHYLLANTHACEAE

Phyllanthus niruri 1.2582 PCASP 1.1875 PCASP NSSP 1.1899 PE 1.2084 PE PE 0.9457 PSI 1.0176 PCI PCI NAG,
POSP,
PE, PSI

POACEAE

Cenchrus ciliaris 1.4427 PCASP 1.4427 PCASP PCASP 0.6695 PX 0.6695 PX PX 0.4641 PSI 0.4641 PSI PSI NAG,
POSP,
PX, PSI

Tragus berteronianus 1.5543 PCASP 1.5731 PCASP PCASP 1.3915 PE 1.4401 PE PE 0.8952 PSI 0.9154 PSI PSI NAG,
PCASP,
PE, PSI

POLYGONACEAE

Coccoloba uvifera 0.1750 PSSP 0.1750 PSSP PSSP 0.1750 PX 0.1750 PX PX 1.0000 SC 1.0000 SC SC NAG,
PSSP,
PX, SC

PORTULACACEAE

Portulaca elatior 1.0711 PCASP 1.2301 PCASP PCASP 0.9741 PX 1.5833 PE PE 0.9095 PSI 1.2871 PCI PSI NAG,
POSP,
PE, PSI

Portulaca oleracea 1.2075 PCASP 0.6937 PSSP PSSP 1.0334 PE 0.6736 PX PX 0.8559 PSI 0.9711 PSI PSI NAG,
PSSP,
PX, PSI

SCROPHULARIACEAE

Capraria biflora 0.7049 PSSP 0.3798 PSSP PSSP 0.7049 PX 0.3607 PX PX 1.0000 SC 0.9496 PSI PSI NAG,
PSSP,
PX, PSI

SOLANACEAE

Datura innoxia 0.8929 PSSP 0.7209 PSSP PSSP 0.7143 PX 0.5765 PX PX 0.8000 PSI 0.7998 PSI PSI NAG,
PSSP,
PX, PSI

Lycium nodosum 0.3871 PSSP 0.1290 PSSP PSSP 0.1935 PX 0.0143 X PX 0.5000 PSI 0.1111 PSI PSI NAG,
PSSP,
PX, PSI

Solanum americanum 0.5514 PSSP 0.6299 PSSP PSSP 0.4507 PX 0.3101 PX PX 0.8174 PSI 0.4922 PSI PSI NAG,
PSSP,
PX, PSI

TALINACEAE

Talinum triangulare 0.4337 PSSP 0.4406 PSSP PSSP 0.3488 PX 0.3535 PX PX 0.8043 PSI 0.8023 PSI PSI NAG,
PSSP,
PX, PSI

Continued

VERBENACEAE

| | | | | | | | | | | | | | | | | |
|---|--------|------|--------|------|------|--------|----|--------|----|----|--------|----|--------|-----|-----|--------------------------|
| <i>Lantana canescens</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.0000 | SI | 0.0000 | SI | SI | NAG, NSSP, X, SI |
| <i>Phyla nodiflora</i> var. <i>reptans</i> | 0.7423 | PSSP | 0.6959 | PSSP | PSSP | 0.7205 | PX | 0.7365 | PX | PX | 0.9707 | SC | 1.0584 | PCI | PCI | NAG, PSSP, PX, PCI |

ZYGOPHILLACEAE

| | | | | | | | | | | | | | | | | |
|----------------------------|--------|------|--------|------|------|--------|---|--------|---|---|--------|-----|--------|-----|-----|-------------------------|
| <i>Guaiacum officinale</i> | 0.0000 | NSSP | 0.0000 | NSSP | NSSP | 0.0000 | X | 0.0000 | X | X | 0.3333 | PSI | 0.3333 | PSI | PSI | NAG, NSSP, X, PSI |
|----------------------------|--------|------|--------|------|------|--------|---|--------|---|---|--------|-----|--------|-----|-----|-------------------------|

B = brevi style individuals, L = Longi style individuals. * Category suggested by: 1- pollen grouped into masses, pollinia (Asclepiadoideae in the Apocynaceae) and (Epidendroideae in the Orchidaceae), and 2- monoecious- hercogamous-dichogamous species (Cnidioscolus urens). PCSM (Partial constrained sexual mating). ¹ = NSSP (Not spontaneous self-pollination); PSSP (Partial spontaneous self-pollination); PCASP (Partial constrained assisted self-pollination). ² X (Xenogamy); PX (Partial xenogamys); PE (Partial endogamy). ³ = SI (Self-incompatibility); PSI (Partial self-incompatibility); SC (Self-compatibility); PCI (Partial cross-incompatibility); CI (Cross-incompatibility). ∞ = indicate values divided by cero (1/BSI ~ 0). ⁴ Information about agamospermy indexes come from appendix 3.

Supplementary Material 3. Frequency of breeding system categories according to some functional plant traits and seral states of the xerophytic community.

| Functional group and habitats | Breeding System Indexes | | | | | | | | | | | | | |
|-------------------------------|-------------------------|----------|-------------------------------------|-----------|---------|----------|----------|-------------------------|-----------|----------|----------------------------|-----------|----------|----------|
| | Agamospermy (IAG) | | Spontaneous self-pollination (ISSP) | | | | | Self-fertility (ISF) | | | Self-incompatibility (ISI) | | | |
| | Categories ¹ | | Categories ² | | | | | Categories ³ | | | Categories ⁴ | | | |
| | NAG | PAG | NSSP | PSSP | SSP | PCASP | OSSP | X | PX | PE | SI | PSI | SC | PCI |
| N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) | |
| Life form | | | | | | | | | | | | | | |
| Trees | 9 (100.0) | 0 (0.0) | 7 (77.8) | 2 (22.2) | 0 (0.0) | 0 (0.0) | 0 (0.0) | 6 (75.0) | 2 (25.0) | 0 (0.0) | 3 (37.5) | 3 (37.5) | 1 (12.5) | 1 (12.5) |
| Shrubs | 5 (83.3) | 1 (16.7) | 3 (37.5) | 4 (50.0) | 0 (0.0) | 1 (12.5) | 0 (0.0) | 3 (37.5) | 5 (62.5) | 0 (0.0) | 0 (0.0) | 6 (100.0) | 0 (0.0) | 0 (0.0) |
| Liana | 7 (100.0) | 0 (0.0) | 6 (66.7) | 2 (22.2) | 0 (0.0) | 0 (0.0) | 1 (11.1) | 7 (77.8) | 2 (22.2) | 0 (0.0) | 3 (42.9) | 3 (42.9) | 0 (0.0) | 1 (14.2) |
| Perennial herbs | 24 (92.3) | 2 (7.7) | 10 (35.7) | 12 (42.9) | 0 (0.0) | 6 (21.4) | 0 (0.0) | 9 (33.3) | 14 (51.9) | 4 (14.8) | 3 (11.5) | 18 (69.3) | 3 (11.5) | 2 (7.7) |
| Annual herbs | 16 (88.9) | 2 (11.1) | 1 (5.3) | 14 (73.6) | 1 (5.3) | 3 (15.8) | 0 (0.0) | 0 (0.0) | 15 (83.3) | 3 (16.7) | 0 (0.0) | 16 (88.9) | 0 (0.0) | 2 (11.1) |
| Succulence | | | | | | | | | | | | | | |
| Non-succulent | 49 (92.4) | 4 (7.6) | 21 (36.2) | 27 (46.6) | 1 (1.7) | 8 (13.8) | 1 (1.7) | 20 (35.7) | 30 (53.6) | 6 (10.7) | 7 (13.2) | 36 (67.9) | 4 (7.6) | 6 (11.3) |
| Succulent | 12 (92.3) | 1 (7.7) | 6 (40.0) | 7 (46.7) | 0 (0.0) | 2 (13.3) | 0 (0.0) | 5 (35.8) | 8 (57.1) | 1 (7.1) | 2 (16.7) | 10 (83.3) | 0 (0.0) | 0 (0.0) |

Continued

| | | | | | | | | | | | | | | |
|--|--------------|-------------|--------------|--------------|------------|--------------|------------|--------------|--------------|-------------|-------------|--------------|-------------|-------------|
| Carbon metabolism | | | | | | | | | | | | | | |
| C ₃ | 45 (91.8) | 4 (8.2) | 20 (37.0) | 26 (48.2) | 1 (1.9) | 6 (11.1) | 1 (1.9) | 19 (36.5) | 28 (53.9) | 5 (9.6) | 6 (12.2) | 34 (69.5) | 3 (6.1) | 6 (12.2) |
| C ₄ | 7 (100.0) | 0 (0.0) | 1 (14.2) | 3 (42.9) | 0 (0.0) | 3 (42.9) | 0 (0.0) | 1 (14.3) | 4 (57.1) | 2 (28.6) | 1 (14.3) | 5 (71.4) | 1 (14.3) | 0 (0.0) |
| CAM | 9 (90.0) | 1 (10.0) | 6 (50.0) | 5 (41.7) | 0 (0.0) | 1 (8.3) | 0 (0.0) | 5 (45.4) | 6 (54.6) | 0 (0.0) | 2 (22.2) | 7 (77.8) | 0 (0.0) | 0 (0.0) |
| Dispersal syndromes^A | | | | | | | | | | | | | | |
| Frugivory ^a | 17 (94.4) | 1 (5.6) | 9 (32.1) | 9 (32.1) | 1 (5.3) | 0 (0.0) | 0 (0.0) | 8 (47.1) | 9 (52.9) | 0 (0.0) | 3 (17.6) | 12 (70.6) | 1 (5.9) | 1 (5.9) |
| Granivorechory ^b | 25 (96.2) | 1 (3.8) | 9 (32.1) | 12 (42.9) | 0 (0.0) | 6 (21.4) | 1 (3.6) | 8 (30.8) | 13 (50.0) | 5 (19.2) | 3 (11.5) | 18 (69.2) | 1 (3.9) | 4 (15.4) |
| Abiotic ^c | 17 (89.5) | 2 (10.5) | 10 (41.7) | 13 (54.2) | 0 (0.0) | 1 (4.2) | 0 (0.0) | 9 (37.5) | 13 (54.2) | 2 (8.3) | 3 (15.8) | 13 (68.4) | 1 (5.3) | 2 (10.5) |
| Epizoochory | 8 (88.9) | 1 (11.1) | 1 (11.1) | 4 (44.4) | 0 (0.0) | 4 (44.4) | 0 (0.0) | 1 (11.1) | 6 (66.7) | 2 (22.2) | 0 (0.0) | 7 (77.8) | 2 (22.2) | 0 (0.0) |
| Pollination systems | | | | | | | | | | | | | | |
| Monophily | 12 (92.3) | 1 (7.7) | 7 (46.7) | 6 (40.0) | 0 (0.0) | 2 (13.3) | 0 (0.0) | 7 (46.7) | 7 (46.7) | 1 (6.6) | 2 (15.4) | 9 (69.2) | 1 (7.7) | 1 (7.7) |
| Oligophily | 11 (84.6) | 2 (15.4) | 6 (37.5) | 7 (43.8) | 0 (0.0) | 2 (12.5) | 1 (6.2) | 6 (42.9) | 6 (42.9) | 2 (14.2) | 2 (15.4) | 9 (69.2) | 1 (7.7) | 1 (7.7) |
| Polyphily | 24 (96.0) | 1 (4.0) | 10 (38.5) | 14 (53.8) | 0 (0.0) | 2 (7.7) | 0 (0.0) | 9 (34.6) | 17 (65.4) | 0 (0.0) | 3 (12.5) | 18 (75.0) | 1 (4.2) | 2 (3.3) |
| Anemophily | 4 (100.0) | 0 (0.0) | 0 (0.0) | 0 (0.0) | 0 (0.0) | 4 (100.0) | 0 (0.0) | 0 (0.0) | 2 (50.0) | 2 (50.0) | 0 (0.0) | 4 (100.0) | 0 (0.0) | 0 (0.0) |
| Habitats | | | | | | | | | | | | | | |
| Late seral (undisturbed) | 18 (94.7) | 1 (5.3) | 13 (56.5) | 8 (34.8) | 0 (0.0) | 2 (8.7) | 0 (0.0) | 12 (57.1) | 8 (38.1) | 1 (4.8) | 4 (21.0) | 14 (73.7) | 0 (0.0) | 1 (5.3) |
| Pioneer (disturbed areas) | 43 (91.5) | 4 (8.5) | 14 (28.0) | 26 (52.0) | 1 (2.0) | 8 (16.0) | 1 (2.0) | 13 (26.6) | 30 (61.2) | 6 (12.2) | 5 (10.9) | 32 (69.5) | 4 (8.7) | 5 (10.9) |
| Overall community | 61 (92.4) | 5 (7.6) | 27 (37.0) | 34 (46.6) | 1 (1.4) | 10 (13.6) | 1 (1.4) | 25 (35.7) | 38 (54.3) | 7 (10.0) | 9 (13.8) | 46 (70.8) | 4 (6.2) | 6 (9.2) |

¹ Agamospermy index categories: NAG = non-agamosperous, PAG = partially agamosperous. ² Spontaneous self-pollination index categories: NSSP = non-spontaneous self-pollinated, PSSP = partially spontaneous self-pollinated, SSP = spontaneous self-pollination, PCASP = partially constrained assisted self-pollination, OSSP = Obligated Spontaneous Self-Pollination. ³ Self-fertility index categories: X = xenogamous, PX = partially xenogamous, PE = partially endogamous. ⁴ Self-incompatibility index categories: SI = self-incompatible, PSI = partially self-incompatible, SC = Self-compatible, PCI = partially cross-incompatible. ** = Statistical analysis was not performed because data set do not fit to statistical test; *** = these results were performed excluding PCSM; PCASP; PE and CI species, respectively. Δ: a = Birds, mammals (including bats), and/or reptiles; b = Birds, mammals and/or ants; c = Abiotic = wind, water, and/or ballistic dispersal. The number of dispersal syndromes exceeds the number of plant species (N = 74) because some species have more than one dispersal syndrome.