



Pollination types and plant reproductive systems of two areas of Venezuelan cloud forests

Nelson Ramírez* and Herbert Briceño

Universidad Central de Venezuela, Facultad de Ciencias, Instituto de Biología Experimental,
Centro de Botánica Tropical. Caracas 1041-A, Venezuela

*e-mail: nramirez220252@gmail.com

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ABSTRACT

The breeding system, sexual system, temporal variation in sex expression and herkogamy and their relation with functional groups and disturbance were investigated in two areas of cloud forests in Venezuela. Pollination types were associated with successional stage and forest area. Bee pollination was the most frequent pollination type in undisturbed areas and both cloud forest localities; however, the percentage of plant species pollinated by bees was remarkably higher in the Altos Pipe than Henri Pittier forest. On the contrary, moth, beetle and bird pollinated species were higher in the Henri Pittier than Alto Pipe forest. Of the 125 plant species, 69.6% were hermaphroditic, 16.0% were monoecious, and 14.4% were dioecious, however, monoecy and dioecy varied considerably according cloud forest area: dioecy was higher in the Altos Pipe forest, while monoecy was higher in Henri Pittier forest. Adichogamy was higher than dichogamy for hermaphrodite and monoecious species in both forest areas. Herkogamous (91.2%) was higher than non-herkogamous species. Many protandrous species tends to have dry fruits and protogynous species fleshy fruits. Outbreeding systems were the most abundant in the plant species studied: no agamospermy (94.7%), non-spontaneous self-pollination (52.3%; 34/65), and xenogamy (61.7%; 37/60) followed by mixed breeding systems, partial spontaneous self-pollination and partial xenogamy. Partial self-incompatibility (59.6%; 31/52) was the higher than self-incompatibility (28.8%; 15/52). Not spontaneous self-pollination, xenogamy and self-incompatibility were mostly shrubs, while mixed breeding systems, partial spontaneous self-pollination and partial xenogamy, and partial self-incompatibility were more abundant in herbaceous life form. Additionally, self-incompatibility index categories were significant associated with fruit texture, self-incompatibility bore mainly fleshy fruits. Accordingly, outbreed is the main form of reproduction in the cloud forest areas, including a representative number of plant species with mixed breeding strategies.

Keywords : Breeding system, community, cloud forest, dichogamy, disturbed areas, herkogamy, life form, pollination, sexual system, Venezuela

Two opposite and extreme plant reproductive strategies are frequently recognized in plant reproduction, outbreeding and inbreeding. Despite of the great diversity of mechanisms promoting outbreeding, dioecy, monoecy, herkogamy, dichogamy, self-incompatibility, there is a considerable number of plant species with different levels of self-fertility, autogamy, self-compatibility and agamospermy (e.g. Ramírez and Seres, 1994, Ramírez and Hokche 2019). The frequency of different reproductive systems at the community level depends on multiple factors, including taxonomic composition, vegetation structure, and disturbance (Ramírez and Brito 1990, Jaimes and Ramírez 1998, Chazdon *et al.* 2003, Ramírez and Hokche 2019). Plant reproductive systems may also be closely related with numerous plant attributes. For example, plant life form is the long-established trait associated with plant breeding systems (Jaimes and Ramírez 1998, Morales and Galetto 2003, Ramírez and Hokche 2019),

together with seed dispersal syndromes, pollination systems, and successional stages (Opler *et al.* 1980, Chazdon *et al.* 2003, Ramírez and Hokche 2019). Comparative analyses of plant life histories show that self-compatibility prevails in early stages, while outcrossing is more the rule in later stages as dicliny, dioecism, and self-incompatibility become more frequent (Opler *et al.* 1980, Tseng *et al.* 2008, Hilje *et al.* 2015). Additional functional groups tend to be correlated with reproductive systems (Ramírez 2005, Vary *et al.* 2011, Godin 2017, Ramírez and Hokche 2019), and could be also affect the patterns of reproduction. Others functional traits may represent attributes linked with sexual and breeding systems: dioecy and frugivory, woody life forms and flowering in the dry period (Muenchow 1987, Ramírez 2005).

Cloud forest represents one of the richest plant species communities in the neotropics. It is recognized that the neotropical cloud forests rank high within the world's most

threatened ecosystems (Hamilton *et al.* 1995), and that the damage done to the is far more likely to be irreversible, because they have low resilience to disturbance (Hamilton *et al.* 1995, Luna-Vega *et al.* 2001). Reproduction is 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 (Hilje *et al.* 2015). Understanding different mating strategies allows us to have knowledge of the susceptibility of plant species to collapse under perturbation scenarios. Studies on reproductive systems at the community level have been conducted mainly in two areas of Venezuelan cloud forests. The first study was carried out in the Altos Pipe forest by Sobrevila and Arroyo (1982), where the high incidence of dioecy occur together with a low level of self-incompatibility among hermaphroditic species. It is concluded that the breeding system spectrum reflects an unpredictable pollination pattern, rather than insufficient pollinator servicing. The second study was carried out for the herbaceous monocots in the Henri Pittier forest (Ramírez and Seres 1994), where monoecy, dichogamy and self-compatibility were the main breeding strategies in the forest. Many other researches on plant reproductive biology have been undertaken in both cloud forest areas, which have led to a more complete range of species along the reproductive spectrum at the community level. Additional studies of reproductive biology in particular plant species have been undertaken in these cloud forest areas (Arroyo and Cabrera 1978, Sobrevila and Arroyo 1982, Sobrevila *et al.* 1983, Ruiz-Zapata 1994, Ramírez and Seres 1994, Jaimes and Ramírez 1999, Castro-Laporte and Ruiz-Zapata 2000, Hokche and Ramírez 2008, Villalobos and Ramírez 2010, Hokche and Ramírez 2016), which have not been included in the frequency of breeding systems at the community spectrum. In this context, this study evaluate the breeding systems for all the plant species previously studied over the entire community spectrum, and also include new assessments, using the same methodology for calculating and comparing breeding systems (Ramírez and Nassar 2016). Specifically, the aim of this study was to determine whether sexual systems, breeding systems, dichogamy, and herkogamy are associated with functional groups; how they are correlated; and how such associations may favor mechanisms that promote outcrossing and inbreeding in a plant community. In addition, how reproductive systems are distributed according to undisturbed and disturbed areas across plant species for the accurate interpretation of plant reproductive strategies. The general goal of this study was thus to characterize the main reproductive systems of the plant species in two cloud forest areas, and to determine which of these were more prevalent.

MATERIAL AND METHODS

Study site and study species— Experimental work was conducted in two cloud forest areas of internal branch of the coastal mountain range in northern Venezuela. Both study areas represent research centers, and exhibit some few differences according to altitude, climate, and floristic composition. The Henri Pittier National Park, Rancho Grande, Aragua State (1,400 m.asl; 10° 21' N; 67° 36' W) is classified as a very humid premontane cloud forest (Ewel *et al.* 1976). Mean annual temperature is 20°C, mean annual precipitation is 1,834 mm, and approximately 249 plant species have been recorded (Huber 1986). The Altos de Pipe Forestry Reserve, Miranda State (1,749 m. asl, 10° 20' N; 66° 55' W) is classified as a cloud forest (Ewel *et al.* 1976, Sobrevila 1978, Buitrón-Jurado 2012). Mean annual temperature is 17.5°C, mean annual precipitation 994 mm, and approximately 154 plant species have been recorded (Sobrevila 1978, Buitrón-Jurado 2012). On the basis of plant species recorded in these areas, there was found 25.6% of floristic similarity between localities. However, it is clearly noted that Henri Pittier forest is a large area of national Park, where forest structure is represented by many large trees, many epiphytes, and an understory comparatively richer in plant species composition than Altos de Pipe forest.

Plant species were selected in order to include the most variety of taxonomic order and family, including different plant life histories for each taxonomic group. A study in preparation (N. Ramírez and H. Briceño) showed that Myrtales order and Melastomataceae family are the main taxa in both forest areas; however, there are not significant effects on sexual systems, herkogamy and dichogamy. A formal phylogenetic analysis was not performed on the data. Instead, dioecy and monoecy frequencies were evaluated in relation to plant clades (APG IV 2016) and its relation with plant life forms as a substitute approximation to assess phylogenetic influence. This approximation allows inferring if dioecy and monoecy are independent of the phylogenetic lineages represented in the study's plant community. A phylogenetic constraint analysis was not performed on the breeding system data, because it has been repeatedly demonstrated that the evolution of self-compatibility, self-incompatibility, and agamospermy are not phylogenetically constrained (Igc *et al.* 2008, Raduski *et al.* 2012, Richards 1997, Bicknell and Catanach 2006). The liability of reproductive mode and life history in many plant families suggests that phylogenetic constraints rarely limit opportunities when ecological conditions require evolutionary shifts in mating system (Barrett 2014).

FUNCTIONAL GROUPS

Plant life-forms—Plant life forms were established according to habit, longevity, stem lignifications, height and ramification type and plant species were classified as tree, shrub, liana, perennial herb, and annual herb (see Ramírez and Seres 1994, for details).

Successional stages—Plant species were also sorted in relation to successional status, where plant species grew in the community: 1- late seral or climax species, and 2- pioneer species. Late seral species were found growing in natural or undisturbed areas, and pioneer were found growing into areas disturbed, like edge road, and mainly disturbed areas formed by gaps originated by falling trees in the forests.

Pollination systems—Information about pollinator agents come from unpublished (N. Ramírez, I. Herrera, C.J. Figueredo and C. Aranguren) and published information (Wasshausen and Arroyo 1976, Sobrevila 1978, Sobrevila *et al.* 1983, Hokche and Ramírez 1990, Ruiz-Zapata 1994, Seres and Ramírez 1995, Guzmán 1995, Castro-Laporte 1999, Villalobos and Ramírez 2010), which were determined following qualitative and quantitative criteria. Observations were completed over more than two flowering periods. The activity of all types of floral visitors was described and then the visitors were captured. Pollinators were distinguished from floral visitors using qualitative criteria of pollen transportation and abundance. Each plant species might be assigned to one or more than one pollination mode. Nine categories of pollination types were distinguished: 1) wind pollination, 2) beetle pollination, 3) fly pollination, 4) bee pollination, 5) wasp pollination, 6) butterfly pollination, pollination by diurnal butterfly, 7) moth pollination, pollination by nocturnal butterfly or moths, 8) bird pollination, and 9) bat pollination. After that, plant species were also categorized dealing principally with the pollination system specialization (Ramírez 2004), the character of visits received (slightly modified from Faegri and Van der Pijl 1979). The following categories were used: 1) polyphily, pollinated by different taxonomic orders of visitors; 2) oligophily, pollinated by more than one family of the same taxonomic order of visitors; and 3) monophily, pollinated by only one species, one genus or different genera of the same taxonomic family. Occurrence of wind pollination was recognized according to floral morphology (Faegri and van der Pijl 1979) 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.

Fruit type—Fruits were classified in relation to texture (fleshy and dry fruit types). Arilated seed of some dry fruits were considered as fleshy fruits. This classification is an approximation of animal and abiotic dispersal mechanisms.

SEXUALITY, HERKOGAMY AND DICHOGAMY

Sexual systems—Plant species were categorized as hermaphroditic, monoecious (monoecious, andromonoecious, and gynomoecious) and dioecious (including some dioecious species based mainly on morphological and functional criteria). Some morphologically hermaphroditic species were considered monoecious or dioecious based on additional criteria (see Ramírez 2005, for details).

Herkogamy—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. Herkogamy was determined when the stigma was positioned at a statistically significant separation from anthers. In this study, occurrence of ordered herkogamy was examined (Webb and Lloyd 1986). Plant species were classified as herkogamous and non-herkogamous.

Temporal variation in sexual expression—Temporal variation in sexual expression was determined following Ramírez (2005). All hermaphroditic, submonoecious, monoecious and hermaphrodite functional-dioecious species were examined to determine if individual flowers or inflorescences (when treated as pollination units) had synchronous or asynchronous male and female phases (Lloyd and Webb 1986). Synchrony of sexual expressions was determined following Ramírez 2005). Plants were categorized as adichogamous (sexual synchrony, following Faegri and van der Pijl 1979), 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* Lloyd and Webb 1986).

PLANT BREEDING SYSTEMS

Experimental pollination tests—Reproductive efficiency under experimental conditions was determined at two levels: 1) fruits developed per total number of flowers, and 2) total number of non-abortive seeds produced by all fruits per total number of ovules (flower number multiplied by 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. Most of the breeding system data come from previous studies

in the same areas of cloud forests (Arroyo 1978, Sobrevila and Arroyo 1982, Sobrevila *et al.* 1983, Ruiz-Zapata 1994, Ramírez and Seres 1994, Jaimes and Ramírez 1999, Castro-Laportte and Ruíz-Zapata 2000, Hokche and Ramírez 2008, Villalobos and Ramírez 2010, Hokche and Ramírez 2016).

Breeding system indexes—Four breeding system indexes (BSI) were determined at fruit and/or seed level following Ramírez and Nassar (2016). 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 level differed, it was opted for the conclusion obtained at seed level.

The Index of Agamospermy (IAG) was determined dividing the results obtained from the agamospermy test by the results obtained from the cross-pollination test (Riveros *et al.* 1996). The Index of Spontaneous Self-Pollination (ISSP) or Automatic Self-pollination Index (Ruiz-Zapata and Arroyo 1978, Sobrevila and Arroyo 1982) was determined 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) (Lloyd and Schoen 1992) was determined 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 (Ruiz-Zapata and Arroyo 1978, Sobrevila and Arroyo 1982) was determined dividing results from the hand self-pollination test by results from the cross-pollination test.

Breeding index categories (BIC)—Five categories for each breeding system index were used (see Ramírez and Nassar 2016 for the meaning of each category): (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 $BSI \sim \infty$). More details about categorization of the BSI, assumptions and exceptional cases may be consulted in Ramírez and Nassar (2016).

In addition, some zoophilous pollination species in which spontaneous self-pollination is avoided as result of morphological traits, monoecy, herkogamy, and protogyny where spontaneous self-pollination is completely avoided ($BSI = 0$) and consequently xenogamy is the main breeding strategy for *Philodendron macroglossum*, *Geonoma* spp. *Asplundia* sp. and *Cyclanthus bipartitus*. In addition, *Epidendrum nocturnum* was also considered in this reproductive category because pollen is grouped into masses, pollinia, which have to be transported by pollinators from the androecium to the stigma in the Epidendroideae (Orchidaceae). This approximation was confirmed by the very low fruit set under natural condition (N. Ramirez unpubl. data), which is an estimate of pollination mediated dependence for fruit production.

STATISTICAL ANALYSIS

A t-test, with degrees of freedom equal to $n-1$ (Sokal and Rohlf 1998), was used to discriminate between Breeding System Index (BSI) values from 0 and 1.0 (see Ramírez and Nassar 2016, for details). When BSI values were higher than $e^{-1.0}$ (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 establish level of dependence between reproductive variables and functional groups, log-linear analyses of frequency were performed using two-way tables (Statsoft 2007). When the log-linear analysis of frequency was significant, residual frequencies, that is, observed minus expected frequencies, were estimated for each cell of the two-factor comparison, and then standardized and tested for significance. This analysis allowed establishing which pairs of variables deviated significantly from expected values (Legendre and Legendre 1993), 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.

RESULTS

Phylogeny and sexual system—Dioecious species ($N=18$) recorded belong to seven clades (APG IV 2016) and 13 plant families (see Appendix 1 for details). Most of dioecious species are trees ($N=13$), followed by shrubs ($N=2$), liana ($N=2$) and perennial herbs ($N=1$). Monoecious species ($N=20$) belong to four different clades and nine families (APG IV 2016), which were well represented in all five life forms: trees ($N=4$), shrubs ($N=3$), liana ($N=4$), perennial herbs ($N=7$), and annual herbs ($N=2$).

Pollination types—Information about the nine assigned pollination types of a total of 55 plant species of the Altos Pipe and 90 plant species from Henri Pittier cloud forests are given in the appendix 1. Pollination type frequency was significantly associated to successional stage ($\chi^2 = 28.2$, $df = 8$, $P < 0.0004$). Bee pollination was the most frequent pollination type in both cloud forests, though bee pollination was higher in disturbed than undisturbed areas (Figure 1A). Moth, beetle and bird pollinated species were higher in undisturbed areas of the cloud forests. Despite of non-statistical test, pollination types and life forms comparison showed that bee pollination was the most abundant pollination type for all life forms. Beetle and wind pollination were also found as an important pollination type for liana, bird pollination for herbs, and moth pollination for trees and shrubs (Table 1). Pollination types differed according to cloud forest locality ($\chi^2 = 18.7$, $df = 8$, $P < 0.015$). The percentage of plant species pollinated by bees was remarkably higher in the Altos Pipe than Henri Pittier forest (Fig. 1B). Additionally, moth, beetle and bird pollinated species were higher in the Henri Pittier than Alto Pipe Forest. Butterfly and bat pollinated species percentage were the lower pollination types in both forest areas.

Table 1. Pollination type richness (N) and their percentage for sexual systems, dichogamy, herkogamy, and life forms.

Plant trait	Pollination type									
	Bee	Wasp	Fly	Butterfly	Moth	Beetle	Bird	Bat	Wind	Total
	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N
Sexual system										
Hermaphrodite	57(54.8)	2(1.9)	3(2.9)	1(1.0)	11(10.6)	1(1.0)	25(24.0)	4(3.9)	0(0.0)	104
Monoecy	2(9.5)	0(0.0)	3(14.3)	0(0.0)	1(4.8)	12(57.1)	0(0.0)	0(0.0)	3(14.3)	21
Dioecy	6(30.0)	4(20.0)	3(15.0)	0(0.0)	0(0.0)	2(10.0)	0(0.0)	0(0.0)	5(25.0)	20
Dichogamy										
Adichogamy	48(55.2)	1(1.2)	2(2.3)	1(1.2)	11(12.6)	1(1.2)	21(24.1)	2(2.3)	0(0.0)	87
Protandry	7(33.3)	1(4.8)	3(14.3)	0(0.0)	1(4.8)	2(9.5)	4(19.1)	2(9.5)	1(4.8)	21
Protogyny	2(13.3)	0(0.0)	1(6.7)	0(0.0)	0(0.0)	10(66.7)	0(0.0)	0(0.0)	2(13.3)	15
Herkogamy										
Herkogamy	58(47.2)	4(3.3)	7(5.7)	1(0.8)	12(9.8)	12(9.8)	20(16.3)	3(2.44)	6(4.9)	123
Non-Herkogamy	5(33.3)	2(13.3)	2(13.3)	0(0.0)	0(0.0)	0(0.0)	5(33.3)	1(6.7)	0(0.0)	15
Life form										
Trees	15(57.7)	2(7.7)	3(11.5)	0(0.0)	3(11.5)	1(3.9)	2(7.7)	0(0.0)	0(0.0)	26
Shrubs	19(46.3)	0(0.0)	2(4.9)	0(0.0)	6(14.6)	4(9.8)	6(14.6)	2(4.9)	2(4.9)	41
Liana	5(33.3)	1(6.7)	0(0.0)	0(0.0)	1(6.7)	4(26.7)	1(6.7)	0(0.0)	3(20.0)	15
Herbs	24(41.3)	3(4.8)	4(6.4)	1(1.6)	2(3.2)	6(9.5)	16(25.4)	2(3.2)	3(4.8)	63

The number of pollination types exceeds the number of plant species because many species were assigned more than one pollination type. The totals for habitats and life forms are not equal because several of the life forms are encountered in more than one habitat. Data distribution did not fit to log-linear test.

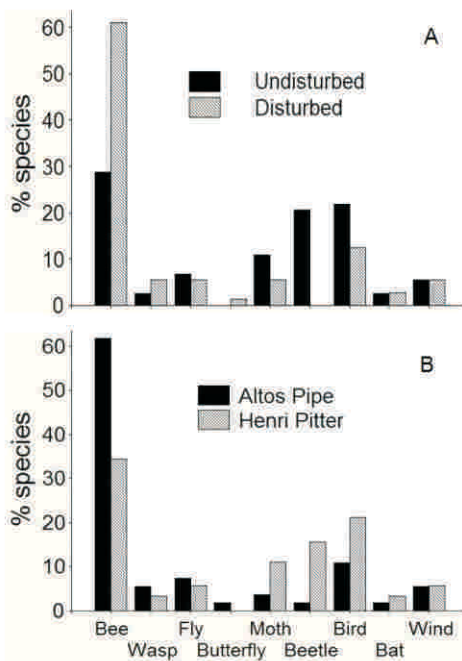


Fig. 1: Frequency distribution of pollination agent classes according to successional stage (A) and cloud forest areas (B).

Sexual system, dichogamy and herkogamy—Information on plant species, taxonomic position, sexual systems, dichogamy, herkogamy, and habitats is compiled in appendix 1. Sexual systems frequencies are statistically associated with cloud forest locality (Table 2). Hermaphrodite species were similarly distributed in both cloud forest areas, however, dioecy was higher in Altos Pipe than Henri Pittier forest; the opposite was found for monoecy. Plant sexual systems varied as a function of the successional stage: dioecy was higher in the late seral than the pioneer stage, however, such trend was not significant.

Herkogamy and dichogamy— The relationship between herkogamy and cloud forests was non-significant (Table 2). Frequency of herkogamy and no herkogamy were identical in both cloud forest areas. Temporal variation in sexual expression was independent of the cloud forest locality, however, protogyny tend to be higher in undisturbed areas. Adichogamy was better represented than dichogamy in hermaphrodite and monoecious species from both cloud forest areas (Table 2). Protandry tended to be more frequent than protogyny in the Altos Pipe forest and similarly distributed in the Henri Pittier forest. Protandry and protogyny were similar

in the Henri Pittier forest. The ratio between the number of herkogamous and dichogamous species was 3.2, a close value to that determined in the Henri Pittier forest (2.86), and lower than that of the Altos Pipe forest (6.5).

Sexual system, dichogamy, and herkogamy—Sexual system, hermaphrodite and monoecy, was significantly associated with temporal variation in sexual expression ($C = 56.3$, $df = 2$, $P = 0.00$). Hermaphrodite species were predominantly adichogamous ($N = 72$, 83.7%), followed by protandrous ($N = 12$, 14.0%) and protogynous ($N = 2$, 2.3%). In contrast, monoecious species were mainly protogynous, with residual frequency significant ($P < 0.05$) ($N = 13$, 65.0%), follow by protandrous ($N = 4$, 20.0%), and adichogamous ($N = 3$, 15.0%). Hermaphrodite species were predominantly herkogamous ($N = 75$, 88.2%) and in a lower frequency non-herkogamous ($N = 10$, 11.8%), and monoecious species were exclusively herkogamous ($N = 18$, 100%). Comparison between

temporal variation in sexual expression and spatial variation in sexual organ was non-significant ($C = 2.9$, n.s.). Adichogamous ($N = 66$, 90.4%), protandrous ($N = 13$, 81.2%), and protogynous ($N = 14$, 100.0%) were mostly herkogamous species.

SEXUAL SYSTEM, DICHOGAMY, HERKOGAMY AND FUNCTIONAL GROUPS ASSOCIATED

Plant sexual system was significantly associated only with life forms and pollination system specificity (Table 2). Dioecy was associated with tree life form, with significant residual, and monoecy was mainly associated with herbs. Hermaphrodite species were mainly monophilous and oligophilous pollinated-species, while monoecious and dioecious species were polyphilous and anemophilous. Sexual system was significantly associated to forest locality (Table 2). Dioecy was higher in the Altos Pipe than Henri Pittier forest, the opposite was found for monoecy.

Table 2. Frequency of sexual systems, temporal sexual expression, and spatial sexual separation according to functional plant traits and seral states of two cloud forest areas.

Functional group and plant communities	Sexuality			Temporal sexual expression			Spatial sexual separation	
	Hermaphrodite	Monoecy	Dioecy	Adichogamy	Protandry	Protogyny	Herkogamy	Non-Herkogamy
	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)
Life form	df=6, $\chi^2 = 36.38$, $P < 0.00001$			df=6, $\chi^2 = 11.83$, n.s.			df=3, $\chi^2 = 6.84$, n.s.	
Trees	11(39.3)	4(14.3)	13(46.4) ^a	11(73.3)	1(6.7)	3(20.0)	19(86.4)	3(13.6)
Shrubs	23(82.2)	3(10.7)	2(7.1)	21(80.8)	4(15.4)	1(3.8)	26(100.0)	0(0.0)
Liana	9(60.0)	4(26.7)	2(13.3)	5(41.7)	3(25.0)	4(33.3)	12(92.3)	1(7.7)
Perennial herbs	41(83.7)	7(14.3)	1(2.0)	35(72.9)	6(12.5)	7(14.6)	39(81.3)	9(18.7)
Annual herbs	3(60.0)	2(40.0)	0(0.0)	3(60.0)	2(40.0)	0(0.0)	5(100.0)	0(0.0)
Pollination System	df=4, $\chi^2 = 13.69$, $P < 0.0084$			df=4, $\chi^2 = 7.40$, n.s.			df=2, $\chi^2 = 0.91$, n.s.	
Monophily	33(91.7)	3(8.3)	0(0.0)	26(72.2)	6(16.7)	4(11.1)	30(83.3)	6(16.7)
Oligophily	19(73.1)	5(19.2)	2(7.7)	18(75.0)	1(4.2)	5(20.8)	22(91.7)	2(8.3)
Polyphily	9(50.0)	5(27.8)	4(22.2)	8(57.2)	5(35.7)	1(7.1)	15(88.2)	2(11.8)
Anemophily	0(0.0)	2(50.0)	2(50.0)	0(0.0)	0(0.0)	2(100.0)	4(100.0)	0(0.0)
Fruit type	df=2, $\chi^2 = 0.51$, n.s.			df=2, $\chi^2 = 12.60$, $P < 0.0018$			df=1, $\chi^2 = 1.82$, n.s.	
Fleshy**	54(67.5)	14(17.5)	12(15.0)	51(76.1)	4(6.0)	12(17.9)	66(91.7)	6(8.3)
Dry	36(73.4)	6(13.3)	6(13.3)	24(61.5)	12(30.8)	3(7.7)	35(83.3)	7(16.7)
Habitat	df=2, $\chi^2 = 3.21$, n.s.			df=2, $\chi^2 = 1.63$, n.s.			df=1, $\chi^2 = 0.46$, n.s.	
Undisturbed	50(64.1)	14(17.9)	14(17.9)	42(66.7)	10(15.9)	11(17.4)	60(87.0)	9(13.0)
Disturbed	37(78.7)	6(12.8)	4(8.5)	33(76.7)	6(14.0)	4(9.3)	41(91.1)	4(8.9)
Community	df=2, $\chi^2 = 4.86$, $P < 0.014$			df=2, $\chi^2 = 4.69$, n.s.			df=1, $\chi^2 = 0.00$, n.s.	
Altos Pipe	47(73.4)	3(4.7)	14(21.9)	40(83.3)	5(10.4)	3(6.3)	52(91.2)	5(8.8)
Henri Pittier	71(71.0)	18(18.0)	11(11.0)	58(66.7)	14(16.1)	15(17.2)	83(91.2)	8(8.8)

¹Perennial and annual herbs were cluster for analyses. ²Excluded from statistical analyses. ** : include arilated seed ^a = Positive residual at $P < 0.01$.

Dichogamy, Herkogamy and associated attributes—Temporal variation in sexual expression was only significantly associated with fruit type. Dry fruit predominated in protandrous species and fleshy fruit were most abundant in protogynous species (Table 2). Herkogamy was not significantly associated with functional traits (Table 2).

Pollination type and sexual traits—Comparisons between sexual traits and pollination types were not statistically supported, however, there were found some interesting trends (Table 1). Bee pollination was the most frequent for Hermaphrodite and dioecious species. Moth and bird pollination were also frequent for hermaphrodite species, wasp and wind pollination for dioecy, and beetle pollination was clearly the highest pollination type for monoecious species. Adichogamous and protandrous species were also pollinated by bees. Additionally, adichogamous species were pollinated by birds and moths. Protandrous species were also pollinated by birds and fly; and protogynous species were mainly pollinated by beetle. Herkogamous species were mostly pollinated by bees, followed by birds and moths. The largest frequencies of non-herkogamous species were pollinated by bees and birds in the cloud forests.

BREEDING SYSTEMS AND ASSOCIATED ATTRIBUTES

Breeding systems—Information about ovule number, flower number, fruit set and seed set under experimental pollination tests for five plant species belonging to four plant families is detailed in table 3. All plant species resulted to be non-agamospermous. *Epiphyllum phyllanthus* was clearly self-

incompatible. Fruit set under self-pollination was slightly higher than cross-pollination for *Rhipsalis floccosa* ssp. *pittieri* and *Tibouchina geitneriana*, however, overall seed set under self-pollination was only higher than cross-pollination for *Tibouchina geitneriana*.

Agamospermy indexes and qualitative categories for 57 plant species are reported in Supporting Information 1 and breeding system indexes and their qualitative categories for 67 species are reported in Supporting Information 2.

Agamospermy—Most plant species studied were non-agamospermous (N = 54; 94.7%) and 5.3% (N = 3) were partially agamospermous (Supporting Information 1). All partially agamospermous species were monophilous pollinated; with fleshy fruit mostly herbaceous species from disturbed areas (Table 4).

Spontaneous self-pollination—Four categories of the index of spontaneous self-pollination (ISSP) were recorded in 65 plant species: non-spontaneous self-pollinated species (ISSP = 0; N = 34), partially spontaneous self-pollinated species ($0 < \text{ISSP} < 1.0$; N = 19), spontaneous self-pollinated species (SSP = 1; N = 3). The lowest frequency was found for partially constrained assisted self-pollinated species ($0 < (1/\text{ISSP}) < 1.0$; N = 9); see Supporting Information 2. Spontaneous self-pollination categories were only significantly associated with life form (Table 4). Partially spontaneous self-pollinated species were mostly herbs. Non-significant trends indicate that most spontaneous self-pollinated and partially constrained assisted self-pollinated species come from disturbed areas and their frequency was higher in the Altos Pipe than Henri Pittier forest (Table 4).

Table 3. Results of experimental tests for five plant species from cloud forests.

FAMILY	Experimental test												
	Ovule/ flower	Number of flower under experimental test					Number of fruit set				Number of seed set		
Species	x	E	SSP	SP	CP	E	SSP	SP	CP	E	SSP	SP	CP
BROMELIACEAE													
<i>Tillandsia complanata</i> ¹	216.13	30	46	30	32	0	32	15	15	0	5,006	2,494	2,701
CACTACEAE													
<i>Epiphyllum phyllanthus</i>	326.27	13	23	26	40	0	0	0	34	0	0	0	9,481
<i>Rhipsalis floccosa</i> ssp. <i>pittieri</i>	11.77	11	53	37	23	0	34	24	20	0	503	278	269
IRIDACEAE													
<i>Trimezia martinicensis</i> ²	50.2	30	43	30	30	0	37	23	28	0	1,454	923	1,050
MELASTOMATACEAE													
<i>Tibouchina geitneriana</i> ³	1,342	34	71	44	37	0	0	25	17	0	0	5,310	6,404

Unpublished information completed by ¹ = I. Herrera, ² = C.J. Figueredo and ³ C. Aranguren. ^{1,2,3} = Plant species studied in the Altos de Pipe forest. Cactaceous species studied in the Rancho Grande Forest. E = Emasculatión; SSP = Spontaneous self-pollination; SP = Hand self-pollination; CP = Cross-pollinations;

Table 4. Frequency of breeding system categories according to some functional plant traits and seral stages for two cloud forest areas.

Functional group and communities 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**	X	PX	PE	SI	PSI	PCI
	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)	N(%)
Life form	****		df=6, $\chi^2 = 13.12$, P < 0.0411				df=3, $\chi^2 = 11.71$, P < 0.0084			df=3, $\chi^2 = 14.19$, P < 0.0027		
Trees	4(100.0)	0(0.0)	2(50.0)	0(0.0)	0(0.0)	2(50.0)	2(50.0)	2(50.0)	0(0.0)	0(0.0)	4(100.0)	0(0.0)
Shrubs	14(93.3)	1(6.7)	12(63.2)	3(15.8)	2(10.5)	2(10.5)	13(81.3)	1(6.2)	2(12.5)	9(64.3)	3(21.4)	2(14.3)
Liana	4(100.0)	0(0.0)	5(100.0)	0(0.0)	0(0.0)	0(0.0)	6(0.0)	0(0.0)	0(0.0)	1(33.3)	2(66.7)	0(0.0)
Perennial Herbs***	29(96.7)	1(3.3)	15(44.1)	13(38.2)	1(3.0)	5(14.7)	15(46.9)	15(46.9)	2(6.2)	5(17.2)	20(69.0)	4(13.8)
Annual Herbs***	2(66.7)	1(33.3)	0(0.0)	3(100.0)	0(0.0)	0(0.0)	1(50.0)	1(50.0)	0(0.0)	0(0.0)	2(100.0)	0(0.0)
Pollination Systems	****		df=4, $\chi^2 = 7.77$, n.s.				df=2, $\chi^2 = 4.04$, n.s.			df=2, $\chi^2 = 2.59$, n.s.		
Monophily	22(88.0)	3(12.0)	11(39.3)	13(46.4)	1(3.6)	3(10.7)	13(52.0)	10(40.0)	2(8.0)	5(21.7)	15(65.2)	3(13.1)
Oligophily	17(100.0)	0(0.0)	14(73.7)	3(15.8)	0(0.0)	2(10.5)	15(83.3)	3(16.7)	0(0.0)	6(40.0)	8(53.3)	1(6.7)
Polyphily	6(100.0)	0(0.0)	4(57.1)	1(14.3)	1(14.3)	1(14.3)	5(71.4)	1(14.3)	1(14.3)	3(50.0)	2(33.3)	1(16.7)
Anemophily*	2(100.0)	0(0.0)	0(0.0)	1(50.0)	0(0.0)	1(50.0)	0(0.0)	1(50.0)	1(50.0)	0(0.0)	1(50.0)	1(50.0)
Fruit texture	****		df=2, $\chi^2 = 4.58$, n.s.				df=1, $\chi^2 = 3.06$, n.s.			df=1, $\chi^2 = 3.76$, P < 0.0488		
Fleshy	33(91.7)	3(8.3)	27(61.3)	10(22.7)	2(4.6)	5(11.4)	28(70.0)	10(25.0)	2(5.0)	13(38.2)	18(53.0)	3(8.8)
Dry	20(100.0)	0(0.0)	7(33.3)	9(42.9)	1(4.8)	4(19.0)	9(45.0)	9(45.0)	2(10.0)	2(11.1)	13(72.2)	3(17.7)
Habitat	****		df=2, $\chi^2 = 5.18$, n.s.				df=1, $\chi^2 = 0.59$, n.s.			df=1, $\chi^2 = 0.53$, n.s.		
Undisturbed	32(100.0)	0(0.0)	24(61.5)	11(28.2)	1(2.6)	3(7.7)	26(66.7)	12(30.8)	1(2.5)	8(25.8)	20(64.5)	3(9.7)
Disturbed	21(87.5)	3(12.5)	10(38.4)	8(30.8)	2(7.7)	6(23.1)	11(52.4)	7(33.3)	3(14.3)	7(33.3)	11(52.4)	3(14.3)
Community	****		df=2, $\chi^2 = 2.47$, n.s.				df=2, $\chi^2 = 1.54$, n.s.			df=2, $\chi^2 = 0.83$, n.s.		
Altos Pipe	24(96.0)	1(4.0)	12(44.4)	6(22.2)	2(7.4)	7(25.9)	12(52.2)	10(43.5)	1(4.3)	7(31.8)	14(63.6)	1(4.6)
Henri Pittier	44(95.6)	2(4.4)	31(55.4)	15(26.8)	3(5.4)	7(12.5)	34(65.4)	15(28.8)	3(5.8)	13(29.6)	26(59.1)	5(11.4)

* : ¹ = NAG (No agamospermy); PAG (Partial agamospermy). ² = NSSP (Not spontaneous self-pollination); PSSP (Partial spontaneous self-pollination); SSP (Spontaneous self-pollination); PCASP (Partial constrained assisted self-pollination). ³ = X (Xenogamy); PX (Partial xenogamy); PE (Partial endogamy). ⁴ = SI (Self-incompatibility); PSI (Partial self-incompatibility); PCI (Partial cross-incompatibility). * = Anemophily, partial endogamy, and partial cross-incompatibility were excluded for statistical analyses. ** = Spontaneous self-pollination and partial constrained assisted self-pollinated categories were clustered for statistical analyses, except for community analysis. *** = Perennial and annual herbs were clustered for statistical analyses. **** = Insufficient information for statistical test.

Self-fertility—Three categories of the index of self-fertility (ISF) were recorded: xenogamy (ISF = 0; N = 37), partial xenogamy (0 < ISF < 1.0; N = 19), and partial endogamy (0 < (1/ISF) < 1.0; N = 4). Self-fertility categories were only significant associated with life form (Table 4). The highest frequency of xenogamy was found in shrubs, and mostly of partially xenogamous species were herbs. Non-significant outcomes showed that xenogamous species had fleshy fruits and partially xenogamous species bear frequently dry fruits

Self-incompatibility—Three categories of the index of self-incompatibility (ISI) were found: partially self-incompatible

(0 < ISI < 1.0; N = 31), self-incompatible (ISI = 0; N = 15), and partially cross-incompatible (0 < (1/ISI) < 1.0; N = 6). The relationships between the categories of ISI and functional groups were only significant for life form and fruit type (Table 4). Shrubs were mostly self-incompatible, while herbaceous species were mostly partially self-incompatible; partial cross-incompatibility was also found in perennial herbs. Self-incompatibility was found related in a large extend with fleshy fruits. Despite of the non-significant outcome, partially cross-incompatible species were more frequent in the Henri Pittier than Altos Pipe Forest.

DISCUSSION

Pollination modes—The frequency of pollination modes in the two areas of cloud forest was dominated by bee with all other pollination modes accounting for less than 22% each. Bee, moth, beetle, and bird pollination frequency differed between the two cloud forest areas examined; and seems to be related to the diversity of plant species, life forms, and successional stage (Ramírez 1989, Ramírez and Brito 1992, Seres and Ramírez 1995, Ramírez 2004). An increase of plant species diversity is accompanied by an increase of pollination modes diversity (Vogel and Westerkamp 1991). The higher plant diversity in the Henri Pittier forest seem to be related with the lower frequency of bee pollination and the comparative large frequency of moth-, beetle-, and bird-pollinated species. An increase in each one of the other pollination modes is matched to a decrease in the relative abundance of bee pollination species (Ramírez 2004). Trends have been proposed for changes in the spectrum of pollination modes throughout the successional stages and the association between life form and pollination mode (Ramírez 2004). Pollination types and life forms showed that bee pollination was the most abundant pollination type for all life forms. However, the abundance of particular life forms in cloud forest areas may affect the frequency distribution of pollination modes. For example, butterfly pollination is frequently found in herbaceous life form from open habitats (Ramírez 2004); the lowest frequency of butterfly pollination could be related with divergent characteristics found in the cloud forests. The abundance of moth, beetle and bird pollination in the Henri Pittier forest and undisturbed areas may be primarily related with life form. Moth pollination was mostly associated with woody species of forest communities (Haber and Frankie 1989, Ramírez 2004), many shrubs from understory of the Henri Pittier forest are moth-pollinated (Castro-Laporte 1999). Similarly, beetle pollination is frequently related with forest condition. Records from other communities indicate that beetle pollination may be one of the most frequent pollination modes in forest conditions (Gottsberger 1989, Irwine and Armstrong 1990, Seres and Ramírez 1995, Ramírez 2004) as recorded in many herbaceous species from the understory Henri Pittier cloud forest (Seres and Ramírez 1995). Bird-pollinated in herbaceous species from understory strata of the Henri Pittier forest may reflect that bird-pollinated species tend to be mostly herbs and shrubs. Bird-pollinated species constitute an important component of plant communities in the neotropics (Snow and Snow 1980), and particularly so in understory tropical forests (Seres and Ramírez 1995, Kato 1996). In fact, the higher frequency of bird pollination in the cloudy forest could be associated with the fact that pollinator birds seem to be more abundant in habitats with a less seasonal climate, dominated

by a benign condition, which is associated with more constant and abundant food resources through the year.

Reproductive systems—Outbreeding and inbreeding strategies and the concomitant mixed breeding strategies documented in both cloud forests exhibited some associations with functional groups and disturbance. High levels of outbreeding strategies, dioecy, herkogamy, non-agamospermy, non-spontaneous self-pollination, xenogamy, and self-incompatibility have a tendency to occur mainly in woody species, occurring in the late successional stage. 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 its influence should be considered negligible. Mixed breeding strategies, counting intermediate strategies, partial spontaneous self-pollination, partially xenogamy, and partially self-incompatibility were found associated with herbaceous species with dry fruits. Inbreeding systems, spontaneous self-pollination, partial endogamy, and partial cross-incompatibility, are associated with herbaceous life forms, polyphilous and anemophilous pollination systems, and dry fruits, growing preferentially in disturbed areas. Breeding system strategies seem to be also independent of phylogenetic effects (Igic *et al.* 2004, Raduski *et al.* 2012, Richards 1997, Bicknell and Catanach 2006).

Sexual systems—The frequency of dioecy and monoecy was different in both cloud forest areas. The largest frequency of dioecy in the Altos de Pipe forest agrees with previous results (Sobrevila and Arroyo 1982). The comparative high incidence of monoecy in the Henri Pittier forest is in concordance with the large count of monoecious-dichogamous species recorded in monocot-herbaceous species in this forest area (Ramírez and Seres 1994). The large frequency of dioecious species agrees with the highest values recorded previously for trees in the Altos Pipe forest (Sobrevila and Arroyo 1982). Such differences may be related with many environmental factors, plant species diversity and composition; however, differences in life form composition between forest areas may also influence such results. Herbaceous life forms were comparatively well represented in the Henri Pittier forest. When plant community was considered according to successional stage, the proportion of dioecious species was significant larger for undisturbed compared to disturbed habitats. The association between sexual system and life form suggest that the frequency of life forms observed in the sample could be considered the proximate cause in the distribution of dioecy and monoecy in the cloud forest species. The highest frequency of dioecy is related to the association between dioecy and woody condition (Vary *et al.* 2011, Schlessman *et al.* 2014, Godin 2017, Ramírez and Hokche 2019) found in the Altos Pipe Forest. On the contrary, monoecy represents a

significant sexual system promoting cross-pollination in the Henri Pittier forest, where the frequency was closely related to that found in the herbaceous-shrubby communities (16.5%; Ramírez and Hokche 2019) and in the Venezuelan Llanos (17.1%; Ramírez 2005). The highest frequency of dioecy in undisturbed areas is related to the association between dioecy and woody condition (Vary *et al.* 2011, Schlessman *et al.* 2014, Godin 2017, Ramírez and Hokche 2019). Pollination system specificity was also significant for sexual system categories. Dioecious species were frequently anemophilous and polyphilous, mostly represented by bees, flies, and wasps, which concur with a previous study (Ramírez and Hokche 2019), while monoecious species were found across varied levels of pollination system specificity. Polyphily and anemophily in dioecious and approximately 50% of monoecious species showed significant generalist pollination systems in diclinous species in the cloud forest areas. In wind-pollinated species, the pollen transport effectiveness is subject to certain levels of imprecision or difficulty for pollination success (Levin 2012); generalist pollination systems, like polyphily, may also be under pollination limitation.

Sexual system, dichogamy and herkogamy—Adichogamy and herkogamy as the most frequent floral traits in the two areas of cloud forests is similar to that found in other tropical communities (Ramírez 2005, Ramírez and Hokche 2019), and suggest that herkogamy is the main devise for avoid self-pollination at the community level. The ratio between herkogamy/dichogamy for the plant species from both cloud forest areas was close to that found in two different geographical areas (Ramírez 2005, Ramírez and Hokche 2019). The similarity in the frequency of dichogamy and herkogamy between contrasting geographic areas suggests general patterns in the mechanisms to avoid the interference pollen-stigma and promote cross-pollination. 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 (Ramírez and Seres 1994, Ramírez and Hokche 2019). The combination of monoecy and dichogamy (85.0%), and hermaphrodite and herkogamy (88.2%) may be important attributes avoiding self-pollination and prevented autogamy in the cloud forests. Therefore, there is only a small proportion of plant species without adaptation for cross-pollination, represented by hermaphrodite–non-herkogamous species.

Spatial and temporal variation in sexual expression—Spatial and temporal variation in sexual expression was independent of nearly all functional traits examined, departing from previous community studies (Ramírez 2005, Ramírez and Hokche 2019). Temporal variation in sexual expression was associated with fruit type only. Protandrous species bore mostly dry fruits, while protogynous species exhibited fleshy fruits, which suggest that protogyny is mainly related with specialized dispersal by frugivory, and protandry seem to have

a more diversified dispersal mechanisms, as wind dispersal occurring in the main families of epiphyte species.

BREEDING SYSTEMS AND CORRELATES

Outbreeding and inbreeding strategies recognized in this study are mainly associated to life forms. Outbreeding strategies, non-agamospermy, non-spontaneous self-pollination, xenogamy, and self-incompatibility were mostly related with shrubs, whereas partial spontaneous self-pollination, partial xenogamy and partial self-incompatibility were related with herbaceous species. Inbreeding strategies, partial constrain assisted spontaneous pollination and partial cross-incompatibility is primarily associated to herbaceous life forms from disturbed areas. In this context, ecological and evolutionary trends of outbreeding and inbreeding strategies are discussed.

Agamospermy—The majority of species examined in the two communities were non-agamospermous. This pattern is consistent with the observed limited occurrence of agamospermy at the community level in many ecosystems (Raduski *et al.* 2012, Ramírez and Hokche 2019), with available records at family level (Firetti 2018), and other surveys (Ramírez and Nassar 2016). Only partially agamospermous species were found in very low frequency in disturbed areas, and may be considered a suitable and evolutionary stable reproductive strategy, because it combines sexual and asexual reproduction (e.g. Richards 1997, 2003, Firetti 2018). Partial agamospermy in herbaceous life form might represent selective forces for asexual seed production in disturbed areas. In fact, variations in the occurrence of agamospermous species at the community level may as well depend of ecological factors such as disturbance (Baker 1978, Ramírez and Hokche 2019) and taxonomical groups (Firetti 2018, Jaimes and Ramírez 1998, Hokche and Ramírez 2008).

Spontaneous self-pollination and self-fertility—The frequency of xenogamy was higher than that of partial xenogamy. Xenogamy is not always directly determined by the absence of autogamy. Some partially spontaneous self-pollinated species may outcome as xenogamous species, because a large amount of fruits and seeds are mainly produced by certain levels of self-incompatibility what can be present in some partially spontaneous self-pollinated species (Ramírez and Nassar 2016). Therefore, the frequency of xenogamy and partial xenogamy according to plant community and life forms were highly corresponded with the frequency of non-spontaneous self-pollinated species and partial spontaneous self-pollinated species respectively. The frequency of xenogamous and non-spontaneous self-pollinated species was higher in shrubs, whereas partially xenogamous and partially spontaneous self-pollinated species were more frequent in herbaceous life forms. Xenogamy is often associated with woody life form; a typical trait of outbreeding tropical species found in late successional species (Ruiz-Zapata and Arroyo

1978, Bawa *et al.* 1985, Morales and Galetto 2003, Ramírez and Hokche 2019). Among the numerous reasons could be related with the opportunity for multiples reproductive episodes in perennial life forms, which may cover unexpected fail in bad times in the following reproductive periods. Partially spontaneous self-pollinated and partially xenogamous species were highly associated with herbaceous species, including annual herbs, growing in disturbed areas; the largest parts of these are recognized pioneer species (Raffl *et al.* 2007, Levin 2012). These breeding categories represent generalized life history strategies of most herbs. Spontaneous self-pollination and partially constrained assisted self-pollination category were found in very low frequencies of herbaceous and woody species. Many of these species come from disturbed areas and suggest that partially spontaneous self-pollination, spontaneous self-pollination and partially constrained assisted self-pollination categories tend to be associated with generalized life history strategies, even though diverse functional groups may depart from colonizing strategies.

Self-incompatibility—Partial self-incompatibility has been interpreted as evidence of high reproductive success, associated with mixed-mating system in natural ecosystems (Ramírez and Nassar 2016), and it is considered an optimal and evolutionary stable breeding strategy (Harder *et al.* 2007). The highest frequency of partially self-incompatible species in both cloud forest areas is mainly associated with the abundance of herbaceous species examined. The high incidence of partial self-incompatibility agrees with partial spontaneous self-pollination and partial xenogamy according to the high frequency of herbaceous species. In this context, partially self-incompatible species may be considered as a generalized plant life history strategy. Self-incompatibility was the second most important category in the overall species, which agree with previous studies in Venezuela using the same index calculation methodology (Ramírez and Hokche 2019), and is related with the occurrence of shrubs and perennial herbs. Accordingly, reproductive systems in the late successional state are characterized by self-incompatible shrubs with fleshy fruits in the cloud forests examined. On the contrary, partially cross-incompatibility was recorded among plant species studied at very low frequency and associated with perennial herbaceous life forms.

CONCLUSIONS

A large quantity of plant species tended to have mixed reproductive systems: the highest number and frequency of plant species were hermaphrodite, adichogamous, and herkogamous. Dioecy, monoecy, and dichogamy were also found as the second most important outbreeding traits: dioecy in the Altos Pipe forest and monoecy and dichogamy in the Henri Pittier forest. Dioecy was associated to trees, polyphily, and anemophily, and dichogamy was associated with fruit

type: protogyny was linked with fleshy fruits and protandry with dry fruits. No agamospermy, no spontaneous self-pollination, and xenogamy were the main outbreeding strategies in plant species of both cloud forests. These reproductive categories were significant for woody species, including self-incompatibility. Mixed breeding system strategies, partial spontaneous self-pollination and partial xenogamy were the following categories found in cloud forests species, and together with self-incompatibility, the most important category of the self-incompatibility index, were associated with herbaceous life form, largely perennial herbs. Inbreeding categories, partial constrained assisted self-pollination, partial endogamy, and partial cross-incompatibility were variedly associated with functional traits and forest areas.

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Appendix 1. Plant family and species, and ecological and reproductive traits of plant species studied in the two localities of cloud forests.

FAMILY species	Locality	Life form	Successional stage	Sexual system	Dichogamy	Herkogamy	Pollination type	Type of visit received	Fruit texture
ACANTHACEAE									
<i>Justicia secunda</i> Vahl	HP	Ph	P	H	PT	H	OR	MO	D
<i>Justicia stipitata</i> Wash. & Arroyo	HP	Ph	L	H	PT	H	ME	MO	D
<i>Mendoncia tovarensis</i> (Klotzsch & H. Karst. ex Nees) Leonard	HP, AP	L	L	H	-	-	-	-	F
<i>Ruellia humboldtiana</i> (Nees) Lindau	HP	Ph	P	H	AD	H	-	-	D
<i>Ruellia macrophylla</i> Vahl	HP	Ph	P	H	AD	H	-	-	D
ADOXACEAE									
<i>Viburnum tinoides</i> L. f.	AP	S	L	H	AD	H	ME	OL	F
ANACARDIACEAE									
<i>Toxicodendron striatum</i> (Ruiz & Pav.) Kuntze	AP	T	L	D	-	NH	ME	OL	F
APOCYNACEAE									
<i>Aspidosperma fendleri</i> Woodson	HP, AP	T	L	H	AD	H	-	-	D
ARACEAE									
<i>Anthurium nymphaeifolium</i> K. Koch & C.D.	AP	Ph	L	H	PG	H	-	-	F
<i>Bouché Philodendron macroglossum</i> Schott	HP	L	L	M	PG	H	CA	MO	F
<i>Xanthosoma undipes</i> (K. Koch & C.D. Bouché) K. Koch	HP	Ph	L	M	PG	H	CA	MO	F
ARALIACEAE									
<i>Schefflera glabrata</i> (Kunth) Frodin	AP	T	L	H	AD	H	ME	OL	F
ARECACEAE									
<i>Bactris setulosa</i> H. Karst.	HP	T	L	M	PG	H	-	-	F
<i>Chamaedorea pinnatifrons</i> (Jacq.) Oersted	HP, AP	S	L	D			CA, AN	PO	F
<i>Geonoma simplicifrons</i> Willd.	HP	S	L	M	PT	H	CA, MI	PO	F
<i>Geonoma spinescens</i> H. Wendl. ex Burret	HP	S	L	M	PT	H	-	-	F
<i>Geonoma tenuis</i> Burret	HP	S	L	M	PT	H	CA, MI	PO	F
<i>Socratea karstenii</i> F.W. Stauffer & Balslev	HP	T	L	M	PG	H	CA, MI	PO	F
ASTERACEAE									
<i>Baccharis trinervis</i> Pers	HP, AP	Ph	P	D		NH	ME, MI, WA	PO	D
<i>Mikania johnstonii</i> B.L. Rob.	HP	L	P	H	PT	H	ME, WA	PO	D

FAMILY species	Locality	Life form	Successional stage	Sexual system	Dichogamy	Herkogamy	Pollination type	Type of visit received	Fruit texture
Oyedaea verbesinoides DC.	AP	T	P	H	PT	NH	MI, ME	PO	D
BEGONIACEAE									
Begonia humilis Dryand.	HP	Ah	L	M	PT	H	ME, AN	PO	D
BORAGINACEAE									
Cordia aristeguietae G. Agostini	HP	S	P	H	AD	H	-	-	F
BROMELIACEAE									
Aechmea fendleri André	HP	Ph	L	H	AD	NH	OR	MO	F
Aechmea lasserii L.B. Sm.	HP	Ph	L	H	AD	NH	OR	MO	F
Catopsis nutans (Sw.) Griseb	HP	Ph	L	H	PT	NH	-	-	D
Guzmania nubigena L.B. Sm.	HP	Ph	L	H	PT	H	-	-	D
Pitcairnia altensteinii (Lk., Kl. & Otto) Lem.	HP	Ph	L	H	AD	NH	OR	MO	F
Tillandsia complanata Benth.	HP, AP	Ph	L	H	AD	NH	OR	MO	D
Vriesea platynema Gaudich.	HP	Ph	L	H	AD	NH	QU	MO	D
Vriesea splendens (Brongn.) Lem.	HP	Ph	L	H	AD	H	QU	MO	D
CACTACEAE									
Epiphyllum phyllanthus (L.) Haw.	HP	Ph	L	H	AD	H	FA	MO	F
Rhipsalis floccosa Salm-Dyck ex Pfeiff. ssp. pittieri (Britton & Rose) Barthlott & N.P. Taylor	HP, AP	Ph	L	H	AD	H	-	-	F
CAMPANULACEAE									
Centropogon cornutus (L.) Druce	HP	Ah	P	H	PT	H	OR	MO	F
Syphocampylus reticulatus (Willd. Ex Roem. & Schult.)	HP, AP	Ph	L	H	PT	H	OR	MO	D
CANNABACEAE									
Trema micrantha (L.) Blume	AP	T	P	M	AD	-	-	-	F
CLEOMACEAE									
Cleome moritziana Klotzsch ex Eichler	AP	Ph	P	M	AD	H	-	-	D
Cleome pilosa Benth.	HP	Ah	P	M	AD	H	ME, FA	PO	D
CLUSIACEAE									
Clusia multiflora Kunth	AP	T	L	D		H	ME	OL	F
COMMELINACEAE									
Tradescantia zanonii (L.) Sw.	HP	Ph	P	H	AD	NH	ME	MO	F
CONVOLVULACEAE									
Merremia macrocalyx (Ruiz & Pavon) O'Donnell	AP	L	L	H	PT	NH	ME	OL	D

FAMILY species	Locality	Life form	Successional stage	Sexual system	Dichogamy	Herkogamy	Pollination type	Type of visit received	Fruit texture
COSTACEAE									
<i>Costus spiralis</i> (Jacq.) Roscoe	HP	Ph	L	H	AD	H	ORN	MO	F
CYCLANTHACEAE									
<i>Asplundia caput-medusae</i> (Hook. f.) Harling	HP	Ph	L	M	PG	H	CA	OL	F
<i>Asplundia fendleri</i> Harling	HP	Ph	L	M	PG	H	CA	OL	F
<i>Asplundia moritziana</i> (Klotzsch) Harling	HP	L	L	M	PG	H	CA	OL	F
<i>Asplundia</i> sp.	HP	L	L	M	PG	-	CA	OL	F
<i>Cyclanthus bipartitus</i> Poit. ex A. Rich.	HP	Ph	L	M	PG	H	CA	MO	F
<i>Evodianthus funifer</i> (Poit.) Lindm.	HP	L	L	M	PG	H	CA	OL	F
CYPERACEAE									
<i>Scleria latifolia</i> Sw.	HP	Ph	P	M	PG	H	AN	AN	D
ERYTHROXYLACEAE									
<i>Erythroxylum amazonicum</i> Peyr.	AP	S	L	H	AD	H	ME	OL	F
EUPHORBIACEAE									
<i>Croton gossypifolius</i> Vahl	AP	T	P	M	PG	H	-		D
<i>Tetrorchidium rubrivenium</i> Poepp.	HP, AP	T	L	D					F
FABACEAE									
<i>Bauhinia rutilans</i> Spruce ex Benth.	HP	L	L	H	AD	H	ME, OR	PO	D
<i>Chamaecrista nictitans</i> var. <i>pilosa</i> (Benth.) H.S. Irwin & Barneby	AP	Ah	P	H	AD	H	ME	OL	D
<i>Crotalaria micans</i> Link	AP	Ph	P	H	PT	H	ME	MO	D
<i>Dioclea guianensis</i> Benth.	AP	L	L	H	AD	H	ME	OL	D
<i>Inga ingoides</i> (Rich.) Willd.	HP	T	P	H	AD	H	FA	-	D
GENTIANACEAE									
<i>Lisianthus calygonus</i> Ruiz & Pav.	HP, AP	S	P	H	PT	H	QU	MO	D
HELICONIACEAE									
<i>Heliconia acuminata</i> Rich.	HP	Ph	L	H	AD	H	OR	MO	F
<i>Heliconia aurea</i> G. Rodr.	HP	Ph	L	H	AD	H	OR	MO	F
<i>Heliconia bihai</i> (L.) L.	HP	Ph	L	H	AD	H	OR	MO	F
<i>Heliconia revoluta</i> (Griggs) Standl.	HP	Ph	L	H	AD	H	OR	MO	F
HYPERICACEAE									
<i>Vismia baccifera</i> (L.) Triana & Planch.	HP, AP	T	P	H	AD	H	ME	OL	F
IRIDACEAE									
<i>Trimezia martinicensis</i> (Jacq.) Herb.	AP	Ph	P	H	AD	H	ME	OL	D
MALPIGHIACEAE									
<i>Byrsonima karstenii</i> W.R. Anderson	AP	S	L	H	AD	H	ME	-	F

FAMILY species	Locality	Life form	Successional stage	Sexual system	Dichogamy	Herkogamy	Pollination type	Type of visit received	Fruit texture
MALVACEAE									
<i>Heliocarpus americanus</i> L.	AP	T	P	D		NH	-	-	D
MARANTACEAE									
<i>Calathea allouia</i> (Aubl.) Lindl.	HP	Ph	L	H	AD	NH	-	-	F
<i>Calathea</i> sp.	HP	Ph	L	H	AD	H	ME	MO	D
<i>Maranta casupito</i> Jacq.	HP	Ph	L	H	AD	H	ME	MO	D
<i>Stromanthe jacquinii</i> (Roem. & Schult.) H. Kenn. & Nicolson	HP	Ph	L	H	AD	H	OR	MO	D
<i>Stromanthe tonckat</i> (Aubl.) Eichler	HP, AP	Ph	L	H	AD	H	ME	OL	D
MARCGRAVIACEAE									
<i>Ruyschia tremadena</i> (Ernst) Lundell	AP	L	L	H	AD	H	-	-	F
<i>Souroubea guianensis</i> Aubl.	HP	L	L	H	AD	H	-	-	F
MELASTOMATACEAE									
<i>Clidemia fendleri</i> Cogn.	HP, AP	S	L	H	AD	H	-	-	F
<i>Clidemia octona</i> (Bonpl.) L. O. Williams Subsp. Guayanensis Wurdack.	HP	S	P	H	AD	H	-	-	F
<i>Graffenrieda latifolia</i> (Naudin) Triana	HP, AP	T	P	H	AD	H	ME	OL	D
<i>Miconia araguensis</i> Wurdack	HP, AP	Ph	P	H	AD	H	ME	OL	F
<i>Miconia ciliata</i> (Rich.) DC.	HP, AP	Ph	P	H	AD	H	ME	MO	F
<i>Miconia dodecandra</i> Cogn.	HP, AP	T	P	H	AD	H	ME	OL	F
<i>Miconia ibaguensis</i> (Bonp.) Triana	AP	S	P	H	PG	H	ME	MO	F
<i>Miconia laevigata</i> (L.) D. Don	AP	S	L	H	AD	H	ME	OL	F
<i>Miconia minutiflora</i> (Bonpl.) DC.	HP	S	P	H	AD	H	ME	MO	F
<i>Miconia sylvatica</i> (Schltdl.) Naudin	HP	S	P	H	AD	H	ME	MO	F
<i>Miconia tuberculata</i> (Naud) Triana	HP	S	P	H	AD	H	ME	OL	F
<i>Tibouchina geitneriana</i> (Schltdl.) Cogn.	HP	Ph	P	H	AD	H	ME	MO	D
MELIACEAE									
<i>Trichilia hirta</i> L.	AP	T	L	D	-	H	ME, MI, WA	PO	F
MYRTACEAE									
<i>Myrcia fallax</i> (Rich.) DC.	AP	S	L	H	AD	H	-	-	F
<i>Myrcia splendens</i> (Rich.) DC.	HP	T	P	H	AD	H	-	-	F
<i>Siphoneugena dussii</i> (Krug & Urb.) Proença	AP	T	L	H	AD	H	-	-	F

FAMILY species	Locality	Life form	Successional stage	Sexual system	Dichogamy	Herkogamy	Pollination type	Type of visit received	Fruit texture
NYCTAGINACEAE Guapira opposita (Vell.) Reitz	AP	T	L	D	-	H	-	-	F
ORCHIDACEAE Epidendrum nocturnum Jacq. Govenia fasciata Lindl. Govenia utriculata (Sw.) Lindl.	HP HP HP	Ph Ph Ph	L L L	H H H	AD AD AD	H H H	- ME ME	- MO MO	D D D
PASSIFLORACEAE Passiflora edulis Sims	AP	L	P	H	AD	H	ME	MO	F
PHYLLANTHACEAE Hyeronima moritziana (Muell.-Arg.) Pax & Hoffm. Margaritaria nobilis L. f. Richeria grandis Vahl	HP, AP HP AP	T T T	L L L	D D D	- - -	H - -	- - -	- - -	F D D
PHYTOLACCACEAE Phytolacca rivinoides Kunth & C.D. Bouché	HP, AP	Ah	P	H	AD	H	-	-	F
POACEAE Olyra latifolia L. Pariaria stenolemma Tutin	HP HP	Ph Ph	P L	M H	PG AD	H H	AN CA, MI	AN PO	D D
POLYGALACEAE Monnina pubescens (Bonpl.) Kunth	HP, AP	Ph	P	H	AD	-	ME	OL	F
PRIMULACEAE Myrsine guianensis (Aubl.) Kuntze Rapanea ferruginea (Ruiz & Pav.) Mez	HP HP, AP	T T	L P	D D	- -	H H	ME, WA -	PO -	F F
RANUNCULACEAE Clematis dioica L.	HP, AP	L	P	D	-	H	AN	AN	D
RUBIACEAE Borreria capitata (Ruiz & Pav.) DC. Coccocypselum lanceolatum (Ruiz & Pav.) Pers. Hillia parasitica Jacq. Palicourea angustifolia Kunth Palicourea crocea (Sw.) Schult. Palicourea fendleri Standl. Palicourea petiolaris Kunth Psychotria costularia (Baill.) Standl. & Steyerm. Rudgea karstenii Standl.	AP HP, AP HP AP HP HP, AP HP, AP AP HP, AP	Ph Ph L S S S S Ph T	P P L P P P P P P	H H H H H H H H H	AD AD PT AD AD AD AD AD AD	H H H H H H H H H	ME, MI, WA, PS - FA - ME-OR ME, OR ME, OR MEL OR, ME, FA	PO - - - PO PO PO OL PO	D F D F F F F F F

FAMILY species	Locality ¹	Life form ²	Successional stage ³	Sexual system ⁴	Dichogamy ⁵	Herkogamy ⁶	Pollination type ⁷	Type of visit received ⁸	Fruit texture ⁹
RUTACEAE <i>Zanthoxylum rhoifolium</i> Lam.	HP	S	L	D	-	-	-	-	F
SAPINDACEAE <i>Matayba towarensis</i> Radlk.	HP, AP	T	L	D	-	-	-	-	D
SMILACACEAE <i>Smilax poeppigii</i> Kunth	AP	L	L	D	-	H	AN	AN	F
SOLANACEAE <i>Cestrum bigibbosum</i> Pittier	HP, AP	S	L	H	AD	H	FA	MO	F
<i>Cestrum megalophyllum</i> Dunal	HP	S	L	H	AD	H	FA	OL	F
<i>Cestrum microcalyx</i> Francey	HP	S	L	H	AD	H	FA	OL	F
<i>Cestrum potaliifolium</i> Dunal	HP	S	L	H	AD	H	FA	OL	F
<i>Cestrum salicifolium</i> Jacq.	HP	S	L	H	AD	H	FA	MO	F
<i>Solanum asperum</i> Rich.	HP, AP	S	P	H	AD	H	ME	-	F
STYRACACEAE <i>Styrax pallidus</i> A. DC.	HP	T	L	H	AD	H	-	-	F
THYMELAEACEAE <i>Daphnopsis americana</i> (Mill.) J.R. Johnst.	HP	T	L	D	-	-	-	-	F
ZINGIBERACEAE <i>Renealmia nicolaioides</i> Loes.	HP	Ph	L	H	AD	H	OR	MO	F

¹ Locality: HP = Henri Pittier forest, AP = Alto Pipe Forest

² Life form: T = tree, S = shrub, L = liana, Ph = perennial herb, Ah = annual herb.

³ Successional stage: L = late seral stage, P = pioneer stage.

⁴ Sexual system: H = hermaphrodite, M = Monoecy, D = dioecy.

⁵ Temporal variation in sexual expression: AD = adichogamy, PT = protandry, PG = protogyny.

⁶ Spatial separation in sexual expression: H = herkogamy, NH = no herkogamy.

⁷ Pollination type: ME = bee pollination, OR = bird pollination, CA = beetle pollination, MI = fly pollination, WA = wasp pollination, FA = moth pollination, QU = bat pollination, PS = butterfly pollination, AN = Wind pollination

⁸ Type of visit received: MO = monophily, OL = oligophily, PO = polyphily, AN = anemophily.

⁹ Fruit texture: F = fleshy, D = dry.

Supporting Information 1. Agamospermy indexes and their qualitative categories for 56 plant species from two cloud forest areas.

FAMILY	species	Agamospermy index ?AGI(sp)? ²				Agamospermy index ?AGI(cp)?				Conclusion AGI ¹
		Fruit level		Seed level		Fruit level		Seed level		
		Index	Category	Index	Category	Index	Category	Index	Category	
ADOXACEAE										
	<i>Viburnum tinoides</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
ARACEAE										
	<i>Xanthosoma undipes</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
ARECACEAE										
	<i>Geonoma tenuis</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
BROMELIACEAE										
	<i>Aechmea lasserii</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Catopsis nutans</i>									
	<i>Pitcairnia altensteinii</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Tillandsia complanata</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Vriesea platynema</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Vriesea splendens</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
CACTACEAE										
	<i>Epiphyllum phyllanthus</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Rhipsalis floccosa</i> ssp. <i>pittieri</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
CAMPANULACEAE										
	<i>Centropogon cornutus</i>	0.1765	PAG(sp)	0.1049	PAG(sp)	*	*	*	*	PAG
	<i>Syphocampylus reticulatus</i>	0.0000	NAG(sp)			0.0000	NAG(cp)	*	*	NAG
CANNABACEAE										
	<i>Trema micrantha</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
CLEOMACEAE										
	<i>Cleome moritziana</i>	0.0000	NAG(sp)	*	*	*	*	*	*	NAG
COMMELINACEAE										
	<i>Tradescantia zanoniana</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
COSTACEAE										
	<i>Costus spiralis</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
CYCLANTHACEAE										
	<i>Asplundia fendleri</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Asplundia moritziana</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Evodianthus funifer</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
CYPERACEAE										
	<i>Scleria latifolia</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
FABACEAE										
	<i>Bauhinia rutilans</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	*	NAG(cp)	*	*	NAG
	<i>Chamaecrista nictitans</i> var. <i>pilosa</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Crotalaria micans</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Dioclea guianensis</i>						NAG(cp)			NAG
HELICONIACEAE										
	<i>Heliconia acuminata</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
	<i>Heliconia revoluta</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG

HYPERICACEAE									
<i>Vismia baccifera</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
IRIDACEAE									
<i>Trimezia martinicensis</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
MARANTACEAE									
<i>Calathea sp.</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Stromanthe jacquini</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Stromanthe tonckat</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
MELASTOMATACEAE									
<i>Graffenrieda latifolia</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Miconia ciliata</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.1756	NAG(cp)	0.7928	PAG(cp)	PAG
<i>Miconia ibaguensis</i>	0.2286	PAG(sp)	0.2441	PAG(sp)	*	*	0.4481	PAG(cp)	PAG
<i>Miconia laevigata</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	*	*			NAG
<i>Miconia sylvatica</i>	0.0000	NAG(sp)	*	*	*	*	*	*	NAG
<i>Miconia tuberculata</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	*	*	NAG
<i>Tibouchina geitneriana</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
MYRTACEAE									
<i>Myrcia splendens</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
ORCHIDACEAE									
<i>Govenia fasciata</i>	0.0000	NAG(sp)	*	*	0.0000	NAG(cp)	*	*	NAG
<i>Govenia utriculata</i>	0.0000	NAG(sp)	*	*	0.0000	NAG(cp)	*	*	NAG
PHYTOLACCACEAE									
<i>Phytolacca rivinoides</i>	0.0000	NAG(sp)	*	*	0.0000	NAG(cp)	*	*	NAG
POACEAE									
<i>Olyra latifolia</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Pariana stenolemma</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
POLYGALACEAE									
<i>Monnina pubescens</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
RUBIACEAE									
<i>Palicourea angustifolia</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Palicourea crocea</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Palicourea fendleri</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Palicourea petiolaris</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
<i>Psychotria costularia</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	0.0000	NAG(cp)	NAG
SOLANACEAE									
<i>Cestrum bigibbosum</i>	0.0000	NAG(sp)				NAG(cp)	*	*	NAG
<i>Cestrum megalophyllum</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	*	*	NAG
<i>Cestrum microcalyx</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	*	*	NAG
<i>Cestrum potaliifolium</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	*	*	NAG
<i>Cestrum salicifolium</i>	0.0000	NAG(sp)	0.0000	NAG(sp)	0.0000	NAG(cp)	*	*	NAG
ZINGIBERACEAE									
<i>Renealmia nicolaioides</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 AGI = Agamospermy index: NAG (Non-agamospermous); PAG (Partially agamospermous). * Not available.

