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Ecological correlates with dioecy in the flora of a tropical premontane wet forest in Costa Rica

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ECOLOGICAL CORRELATES WITH DIOECY IN THE FLORA OF A TROPICAL
PREMONTANE WET FOREST IN COSTA RICA

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ABSTRACT

There is a considerable disagreement about the selective forces that have led to the evolution of dioecy (i.e., the condition of having separate male and female flowers on separate plants). Historically, selection to enforce outcrossing has been the primary explanation despite there being little empirical evidence. Hence, many scientist argue that the selection of dioecy is driven by ecological traits that influence male and female fitness and seed dispersal. The objective of this study was to examine the association between plant sexual system (particularly, dioecy) with various ecological traits for the flora of a tropical premontane wet forest in Costa Rica. Our study included 313 angiosperm species in 216 genera and 83 families that were characterized for plant sexual system, growth form, flower size, fruit type, and seed number. Fisher's exact tests were conducted to determine the relationship between each of the ecological characteristics and plant sexual systems at the species- and generic-level. The null hypothesis for all comparisons is that the proportionate representation of hermaphroditic, monoecious, or dioecious species in the various categories is not significantly different from the distribution of species for the entire flora. Of the total 313 species used in this study, 229 (73.2%) were hermaphroditic, 41 (13.1%) were monoecious, and 43 (13.7%) were dioecious. In analyses of species, dioecy was associated with woody growth ($X^2 = 8.53$; $P = 0.03$); tiny flower size ($X^2 = 7.37$; $P = 0.04$), few seeds ($X^2 = 13.82$; $P < 0.001$), and fleshy fruit ($X^2 = 9.18$; $P = 0.003$). Analyses of genera, yielded similar results except there was no association with woody growth. Our results agree with those of other published works on regional floras and suggest that dioecy is heavily driven by 1) woody growth (i.e., the long-lived, perennial growth form), 2) flower size (i.e., tiny, inconspicuous, flowers possibly pollinated by generalized, non-specific pollinators), 3) fruit and seed characteristics (i.e., fleshy, single-seeded fruits that are often dispersed by specialized frugivores, resulting in "high quality" dispersal).

INTRODUCTION

The evolution of plant sexual systems and the development of dioecy are fundamental questions in evolutionary and reproductive ecology (Bawa, 1980; Bawa and Beach, 1981; Matallana et al., 2005; Gao et al., 2012). Bawa (1980) argued for the importance of understanding the evolution of the sexual system of dioecy. While early researchers proposed that outcrossing was the principle selective force responsible for its evolution (e.g., Darwin, 1877; Baker, 1959; Darlington, 1958; Bawa, 1980; Bawa and Beach, 1981; Flores and Schemske, 1984), Bawa (1980) and Bawa and Beach (1981) suggested additional ecological factors, such as resource allocation, seed dispersal, plant pollination, and seed/fruit dissemination also influenced the evolution of dioecy.

Plant mating systems are varied and can include genetic systems that enforce obligate selfing or obligate outcrossing. Superimposed on these genetic systems are morphological mechanisms that result in flowers being bisexual, male or female. This paper addresses the differences in floral morphology involved in hermaphroditic, monoecious, and dioecious species. Hermaphroditic plants produce bisexual flowers that have both male and female reproductive structures (i.e., a perfect flower). Monoecious plants are characterized as having separate male and female flowers on the same plant (i.e., corn, *Zea mays*) while dioecious plants are characterized as having separate male and female flowers on separate plants (i.e., American ivy, *Ilex opaca*). Botanically, both monoecious and dioecious plants are considered imperfect flowers because they are missing either male or female reproductive structures. Related plant sexual systems based on floral morphology include gynodioecy and androdiecy. Gynodioecious and androdieciou plants are composed of female and hermaphroditic plants and of male and

hermaphroditic plants, respectively. These two related sexual systems are very rare among flowering plants ($< 1\%$) (Caruso et al., 2016) and; therefore, are not considered in this study.

The vast majority of all flowering plants worldwide are hermaphroditic (Gross, 2005; Matallana et al., 2005; Igic et al., 2008; Réjou-Méchain, 2015). In contrast, monoecious and dioecious plants make up only 4% and 6% of flowering plants, respectively, and are, therefore, considered relatively rare (Renner and Ricklefs, 1995). In the absence of genetic self-incompatibility, hermaphroditic plants have the ability to self-fertilize; whereas, dioecious plants are forced to outcross. This process requires the inherently risky prospect of pollen transfer from one plant to another (Igic et al., 2008; Renner, 2014; Schlessman et al., 2014). Although dioecy is globally rare, dioecious species are spatially unevenly distributed; they tend to be more common in the tropics, particularly insular tropical islands (Bawa, 1980; Flores and Schemske, 1984; Renner and Ricklefs, 1995; Sakai and Weller, 1999; Vary et al., 2011; Schlessman et al., 2014).

Charles Darwin (1877) was the first botanist to comprehensively document sexual systems in plants (Bawa, 1980; Givnish, 1980; Bawa and Beach, 1981; Matallana et al., 2005; Nazareno et al., 2013). His work along with works that blended Darwinian thinking, Mendelian genetics, and our understanding of genes and genetic change (i.e., the synthetic theory of evolution) lead scientists to presume that dioecy was largely an outcrossing mechanism for genetic recombination (Bawa and Beach, 1985; Ibarra-Manriquez and Oyama, 1992; Gross, 2005; Matallana et al., 2005; Chen and Li, 2008; Vary et al., 2011). In this context, dioecy was thought to have evolved as a means to avoid self-fertilization which can produce offspring of low-fitness due to the presence of recessive deleterious alleles (“inbreeding depression”). In contrast, more recent models propose that sexual systems like dioecy do not invoke outcrossing

as the main selective force but instead involve selection due to ecological constraints (Bawa, 1980; Givnish, 1980; Bawa and Beach, 1981; Flores and Schemske, 1984; Renner and Ricklefs, 1995; Matallana et al., 2005; Chen and Li, 2008; Senarath, 2008; Vary et al., 2011; Schlessman et al., 2014). These later models propose trade-offs between male and female function, such as when mating displays enhance male fitness but decrease female fitness. Hence, instead of being driven by the avoidance of inbreeding, the evolution of dioecy is driven by 1) the ability of the male parent to disperse pollen and the female parent to provide nutritional resources to developing embryos, seeds, and fruits, and 2) the constraints of pollinators and pollinator systems (Bawa and Beach, 1981).

There is little empirical evidence for outcrossing being the principle driving factor responsible for the evolution of dioecy (Bawa, 1980). Bawa and Beach (1981) noted that the outcrossing hypothesis as the sole driving force behind dioecy does not account for the tremendous diversity of sexual systems in plants. Furthermore, Bawa (1980) claims that the evolution of dioecy focuses on the process of outcrossing itself, which influences other selective pressures, such as processes of pollination and seed dispersal. In addition, resource allocation among male and female reproduction is found to be another selective pressure (i.e., female unisexual flowers exhibit a higher frequency than male flowers where high resources are available) (Gao et al., 2012). With regard to pollination, it is suggested that generalist pollinators favor dioecious plants more than hermaphroditic plants (Bawa, 1982; Renner and Ricklefs, 1995; Soares et al., 2014). More generalist pollinators can transfer pollen for more than one plant species, which favors higher success favoring more success in dioecious plants.

Dioecy has evolved multiple times in many plant lineages (Renner and Ricklefs, 1995). Charlesworth and Charlesworth (1978) proposed a model for the evolution of dioecy that

assumed two mutations influencing male and female fertility and likely assumed an inversion event that would prevent genetic recombination. The female haplotype carries a recessive male-sterility allele which is usually the first mutation to occur (Vyskot and Hobza, 2015), while the dominant male-determining chromosome would carry female-sterility alleles. As a result, hermaphrodites would evolve into dioecious species via a gynodioecious intermediate (Charlesworth and Charlesworth, 1978; Charlesworth, 2002).

The flora of the tropics have a high frequency of dioecious species compared to temperate and continental floras and have often been used to explore the association between ecological features and sexual system in flowers (Ibarra-Manriquez and Oyama, 1992; Matallana et al., 2005; Senarath, 2008; Schlessman et al., 2014). These regions are known for their species richness and diversity, low population densities, and high frequency of animal pollination; all of which influence gene flow (Bawa, 1980; Bawa et al., 1985; Chen and Li, 2008; Renner, 2014). For example, the increase in spacing between individual plants due to low population density imposes longer travel for pollinators (Bawa et al., 1985). Both species richness and cross-pollination are suggested to correspond with dioecy being found more commonly in tropical areas.

In the tropical floras, dioecy has been associated with a number of ecological features including 1) woody growth habit (Bawa, 1980; Givnish, 1980; Bullock, 1985; Renner and Ricklefs, 1995; Matallana et al., 2005; Senarath, 2008; Vary et al., 2011; Schlessman et al., 2014), 2) small inconspicuous flowers (Ibarra-Manriquez and Oyama, 1992; Renner and Ricklefs, 1995; Chen and Li, 2008; Senarath, 2008; Vary et al., 2011; Schlessman et al., 2014), 3) fleshy fruit (Bawa, 1980; Givnish, 1980; Ibarra-Manriquez and Oyama, 1992; Renner and Ricklefs, 1995; Matallana et al., 2005; Senarath, 2008; Vary et al., 2011; Schlessman et al.,

2014; Caruso et al., 2016), and 5) endemism (Senarath, 2008). In addition, dioecious species may be favored in insular, island habitats because of the advantages of enforced outcrossing and the ecological advantages associated with unspecialized pollination syndromes and perennial habits (Bawa, 1980; Vary et al., 2011).

The ecological correlates of monoecy have not been studied as extensively as those of dioecious plants. This is largely because of the low frequency of monoecy in tropical regions; However, some studies have shown monoecious plants to be associated with 1) either woody (Chen and Li, 2008; Vary et al., 2011), vine (Renner and Ricklefs, 1995), or herbaceous growth habit (Senarath, 2008), 2) small flowers (Senarath, 2008; Vary et al., 2011), and 3) many-seeded, dry fruits (Flores and Schemske, 1984; Gross, 2005; Chen and Li, 2008; Senarath, 2008; Vary et al., 2011).

The objective of this study was to examine the association between plant sexual system (particularly, dioecy) with the ecological traits of plant growth form, flower size, fruit type, and seed number in a tropical premontane wet forest in Costa Rica. Regional floras are important to understanding plant sexual systems and their ecological correlates, not because they reveal evolutionary mechanisms or selective pathways, but because they provide the basis for testable hypotheses. Specifically, we had the following objectives: 1) determine the frequency distribution of hermaphroditic, monoecious, dioecious sexual systems of the flora of Los Cusingos, 2) quantify the associations between sexual systems and several morphological and ecological traits, and 3) compare the frequency distribution of sexual systems with that of other tropical floras. The goal of this study is to support either the outcrossing or ecological-correlates hypotheses as the primary driving force for the evolution of dioecy.

MATERIALS AND METHODS

Study Site

Refugio de Aves Dr. Alexander Skutch, (hereafter referred to as Los Cusingos) is a 77 hectare protected preserve in the Río General Valley of southern Costa Rica, managed by the Tropical Science Center in San José. Los Cusingos is one of the last remaining forest fragments in the valley of the Río General with an elevation that ranges from 650 to 750 meters. The dry season in Los Cusingos extends from December through April, and the rainy season from May to late November. Rainfall averages less than 50 mm per month during the dry season, and greater than 150 mm (up to 200 mm or more) during the rainy season. The annual precipitation is about 2700 mm within the area. The average monthly daytime temperatures range from 27°C during the rainy season to 31°C during the dry season (World Weather Online, 2014). Los Cusingos is also notable for its abundant bird life (>300 bird species) and for the presence of several large rock formations with Native American petroglyphs (Jones et al., 2015). The area surrounding Los Cusingos is heavily impacted by agriculture (e.g., coffee, sugar cane, and pineapple), in addition to housing and commercial enterprises. The forests within the Río General Valley have been destroyed over the last sixty years with few fragments remaining, including Los Cusingos. These few fragments continue to hold on to the floristic composition of this area unique to Costa Rica. Los Cusingos closely corresponds the tropical premontane wet life zone in the Holdridge Life Zone System (Holdridge, 1967) and represents a portion of the once larger unique forest that occupied the region (Jones et al., 2015).

Species List

The majority of the plant species included in this study were taken from a botanical survey published by Jones et al. (2015). This botanical survey was the first comprehensive study

of the flora of Los Cusingos. It documented 314 species of woody and/or climbing plants. In addition to these species, our study included herbaceous plants that had been collected at Los Cusingos in 2007 to 2010 but were not part of the Jones et al (2015) study (R. Jones, personal communication) for a total of 529 species. Herbarium specimens of the plants of Los Cusingos are currently maintained at the Eastern Kentucky University Herbarium under authority of Ronald Jones in the Department of Biological Sciences. After the removal of non-angiosperm (i.e., gymnosperms, ferns), exotic, or unidentified species, our final list of plants used in this study totaled 313 angiosperm species. See Appendix I for complete list of angiosperm species used in this study.

Data Collection

Herbarium specimens, plant manuals (Hammel et al., 2003a; Hammel et al., 2003b; Hammel et al., 2007; Hammel et al., 2010; Hammel et al., 2014; Hammel et al., 2015), field guide books (Gentry, 2003; Zuchowski, 2005; Gargiullo, 2008; Condit, 2011), and Internet resources were used to determine the following characteristics: sexual system, growth habit, flower size, seed number, and fruit type for each genera and for each species.

Sexual system: All species were classified as hermaphroditic, monoecious, or dioecious based on floral morphology and distribution of flowers. Species were classified as hermaphrodites when bisexual flowers were present, monoecious when separate male and female flowers (unisexual) were present on the same individual, and dioecious when female and male flowers were present on different individuals. Sexual systems like androdioecy/gynodioecy and andromonoecy/gynomonoecy which are variations on the aforementioned classifications were not common in our study and were categorized as dioecious or monoecious, respectively. Genera with mixed sexual systems were classified as hermaphroditic, monoecious, or dioecious

based on the most common sexual system exhibited similar to the classification methods described in Flores and Schemske (1984). For example, a genus that included 3 dioecious species and 1 hermaphroditic species was classified as dioecious.

Growth habit: Species were classified as either tree, shrub (or treelet), vine, or herb.

Trees are those woody species with a single main stem that are known to reach heights of 5 to 30 m. Shrubs (including epiphytic shrubs) are those woody species that are multistemmed from the base and known to reach heights of less than 5 m. Vines are those species that climb or scramble on other vegetation, and herbs are those species that lacked woody growth

Flower size: Flowers were classified based on size intervals similar to those proposed by Senarath (2008): tiny (< 1cm), small (1-3cm), medium (3-5cm) or large (5cm +).

Fruit Type: Fruit type was categorized as either fleshy or dry according to the definition of Ibarra-Manriquez et al. (1992). A fleshy fruit was defined as 1) having fleshy exocarp, 2) being surrounded by fleshy pulp, or 3) having seeds with an attached aril. In contrast, a dry fruit was defined as a fruit that is dry at maturity.

Seed Number: Species were classified as either being 1-seeded or many-seeded. In some cases, the number of seeds per fruit was variable. For example, a species might be listed as having 1 to 3 seeds. These species were categorized as 1-seeded. In cases where the species was listed as having 1 to ≥ 4 seeds, the species was categorized as many-seeded.

Statistical Analysis

The frequency distributions of hermaphroditic, monoecious, dioecious taxa within growth form, flower size, seed number, and fruit type were compared to that of the entire flora with Fisher's exact test calculated with StatXact 11 (Cytel, Cambridge, MA). The Fisher's exact test is a type of contingency table analysis that tests whether categorical variables (i.e., growth habit

and sexual systems) are associated with each other. The null hypothesis for all comparisons is that the proportionate representation of hermaphroditic, monoecious or dioecious species in the various categories is not significantly different from the distribution of species for the entire flora. To take into account the phylogenetic effect on these associations (i.e., non-independence of the evolution of sexual system among related taxa), we repeated the analysis at the generic levels. Hence, genera were categorized for sexual system, growth form, flower size, seed number, and fruit type. For cases in which a genus exhibited multiple phenotypes amongst its species, the most common phenotype was used to characterize the genus.

RESULTS

Taxonomic Summary of the Flora:

The flora used in this study included 313 species, belonging to 216 Genera and 83 families (Figure 2). Only 6 out of the 313 species present at Los Cusingos were found to be endemic to Costa Rica; hence, the role of endemism on the evolution of plant sexual system was not be address in this study.

Common Plant Families: The seven most common plant families which included 119 species were Melastomatace, Fabaceae, Rubiaceae, Malvaceae, Solanaceae, Sapindaceae, and Moraceae (Figure 3a). Five of these families--Solanaceae, Malvaceae, Rubiaceae, Fabaceae, and Melastomatac--were comprised of all hermaphroditic species, while the other two families--Moraceae and Sapindaceae--had both monoecious and dioecious species present, with monoecious as the most common. These common families consisted of a range between 9 to 33 species, making up 38.0% of the total species in the flora found in these specific families.

Common Plant Genera: The six common genera which included 45 species were *Inga*, *Clidemia*, *Ficus*, *Piper*, *Psychotria*, and *Miconia* (Figure 3b). Five of these genera--*Inga*, *Clidemia*, *Piper*, *Psychotria*, and *Miconia*--had all hermaphroditic species, while only one (*Ficus*) had only monoecious species. None of these genera were comprised of dioecious species. The number of species in each genera ranged from 5 to 14 species, making up 14.4% of the total species within the total flora.

Frequency of Plant Sexual System: Of the total 313 species used in this study, 229 (73.2%) were hermaphroditic, 41 (13.1%) were monoecious, and 43 (13.7%) were dioecious (Figure 4a). Of the total 218 genera, 160 (74.1%) were hermaphroditic, 24 (11.1%) were monoecious, and 34 (15.7%) were dioecious (Figure 4b). Of the total 83 families, 55 (75.3%) were hermaphroditic, 6 (8.2%) were monoecious, and 12 (16.4%) were dioecious (Figure 4c). For the summary of family statistics, 10 of the families were not included in percentages of sexual systems due to overlap with multiple species within the same family belonging to more than one sexual system: Araceae (hermaphroditic and monoecious), Arecaceae (monoecious and dioecious), Clusiaceae (hermaphroditic and dioecious), Euphorbiaceae (monoecious and dioecious), Loranthaceae (hermaphroditic and dioecious), Meliaceae (monoecious and dioecious), Moraceae (monoecious and dioecious), Sapindaceae (monoecious and dioecious), Sapotaceae (hermaphroditic and dioecious), and Verbenaceae (hermaphroditic and dioecious).

Association of Sexual System with Growth form: Of the total 313 species, 116 (37.1%) were trees, 110 (35.1%) were shrubs, 59 (18.8%) were vines, and 28 (8.9%) were herbs (Table 1). The distribution of growth habit was significantly associated with sexual system only at the species level ($X^2 = 19.2$, $P = 0.003$), and the frequency of hermaphroditic, monoecious, and dioecious species and genera varied between different growth forms (Figure 5a and 6a). At the

species level, there was an association between dioecy and growth habit (Table 1, $X^2 = 8.53$, $P = 0.03$). Dioecy occurred more frequently than expected, and we rejected the null hypothesis that states the proportionate representation of dioecious taxa among different growth forms is not significantly different from the distribution for the entire flora. Of the total 206 genera included in our analysis, 83 (40.3%) were trees, 64 (31.1%) were shrubs, 40 (19.4%) were vines, and 19 (9.2%) were herbs, each with varying frequencies of hermaphroditic, monoecious, and dioecious genera (Table 2) (Figure 6a). In contrast to the analysis of species, there was no association between dioecy and growth habit in the analysis of genera (Table 2, $X^2 = 5.90$, $P = 0.11$). There were no other significant associations in the comparison of sexual system and growth for either the analysis of species or genera (Table 1 and 2).

Association of Sexual System with flower size: Of the total 313 species, 196 (62.6%) had tiny flowers, 79 (25.2%) had small flowers, 19 (6.1%) had medium flowers, and 19 (6.1%) had large flowers (Table 1). The distribution of flower size was significantly associated with sexual system ($X^2 = 21.0$, $P < 0.001$ and $X^2 = 16.51$, $P = 0.006$ for analyses of species and genera, respectively) and the frequency of hermaphroditic, monoecious, and dioecious species and genera varied between different flower sizes (Figure 5b and 6b). Of the 204 genera, 118 (57.8%) had tiny flowers, 55 (27.0%) had small flowers, 17 (8.3%) had medium flowers, and 14 (6.9%) had large flowers (Table 2). There was an association between dioecious and flower size at the species level (Table 1, $X^2 = 7.37$, $P = 0.04$), as well as at the generic level (Table 2, $X^2 = 7.66$, $P = 0.04$). Dioecious plants had higher high proportions of tiny flowers than expected. There were no other significant associations in the comparison of sexual system and flower size for either the analysis of species or genera (Table 1 and 2).

Association of Sexual System with seed number: Of the total 313 species, 117 (37.4%) had 1-seeded fruit and 196 (62.6%) had many-seeded fruits (Table 1), while 79 (37.1%) and 134 (62.9%) genera had 1-seeded fruit and many-seeded fruits, respectively (Table 2). The distribution of seed number was significantly associated with sexual system at both the species ($X^2 = 32.35$, $P < 0.001$) and genera levels ($X^2 = 19.81$, $P < 0.001$), and the frequency of hermaphroditic, monoecious, and dioecious species and genera varied with seed number (Figure 5c and 6c). Both at the species and generic level, there was an association between dioecious and seed number (Table 1, $X^2 = 13.82$, $P < 0.001$; Table 2, $X^2 = 11.05$, $P = 0.001$). Dioecious taxa were proportionally more frequently 1-seeded than expected for both species and generic levels. There was an association between seed number and hermaphroditism and monoecy at the species level (Table 1, $X^2 = 5.30$, $P = 0.03$ and $X^2 = 6.61$, $P = 0.01$, respectively). Hermaphroditic species were proportionally more frequently many-seeded than expected, while monoecious species were proportionally more frequently 1-seeded than expected.

Association of Sexual System with fruit type: Of the total 313 species, there were 199 (63.6%) and 114 (36.4%) species with fleshy fruits and dry fruits, respectively (Table 1). Of the total 213 genera, 124 (58.2%) and 89 (41.8%) had fleshy and dry fruits, respectively (Table 2). The distribution of fruit type was significantly associated with sexual system for both species ($X^2 = 12.13$, $P < 0.001$) and genera ($X^2 = 16.44$, $P < 0.001$), and the frequency of hermaphroditic, monoecious, and dioecious species and genera varied between different fruit types (Figure 5d and 6d). Dioecy was associated with fleshy fruit in analyses at both the species (Table 1, $X^2 = 9.18$, $P = 0.003$) and genera levels (Table 2, $X^2 = 11.65$, $P = 0.001$); dioecious proportionally found more fleshy fruit than expected at both the species and generic levels. There were no other

significant associations in the comparison of sexual system and fruit type for either the analysis of species or genera (Table 1 and 2).

DISCUSSION

The frequency of the sexual systems of the flora of the tropical premontane wet forest at Los Cusingos were similar to those of 11 other regional floras with sample sizes of 139 to 3529 species (Table 3). These studies reported hermaphroditism as the most common sexual system (60-79%) with monoecy and dioecy being far less frequent (9-22% and 6-26%, respectively). Similarly, the flora of Los Cusingos had a preponderance of hermaphroditic species (73.2%) and lower, but evenly distributed, frequencies of monoecious (13.1%) and dioecious species (13.7%). While the frequencies of monoecious and dioecious species at Los Cusingos were similar to the frequencies reported by Bullock (1985), tropical floras often report a higher incidence of dioecy than of monoecy (Ashton, 1969; Ibarra-Manriquez and Oyama, 1992; Matallana et al., 2005; Chen and Li, 2008), especially in tropical island floras (Schlessman et al., 2014) (Table 3). At Los Cusingos, the relative distribution of sexual systems for genera and families were similar to that of species, although monoecious and dioecious species were not as evenly distributed (Figure 4). Dioecious species are hypothesized to be more common in the insular tropical habitats like Los Cusingos than temperate habits due to the ecological advantages of associations with unspecialized pollination syndromes and the perennial habit (the latter of which is more common in the tropics) (Bawa, 1980; Vary et al., 2011).

In this study, dioecy was associated with woody growth (i.e., tree habit); there were significantly more dioecious tree species than expected. This is similar to what was reported for other tropical floras (Givish, 1980; Bullock, 1985; Renner and Ricklefs, 1995; Matallana, 2005; Senarath, 2008; Vary et al., 2011; Schlessman, 2014; Caruso et al. 2016). Generally, there is a

higher incidence of woody species in tropical floras than temperate ones (Bawa, 1980; Givnish, 1980; Vamosi and Vamosi, 2004; Matallana et al., 2005; Chen and Li, 2008), and it has been reported that of the tree and shrub species in any one tropical forest site, 16-28% are dioecious (Ashton, 1969; Flores and Schemske, 1984; Bullock, 1985; Queenborough et al., 2007). The high incidence of dioecy in tropical floras may be due in part to the association between dioecy and perennial habit (Bawa, 1980).

Dioecy was associated with flower size such that flowers less than 1 cm in length were more frequently associated with dioecy than predicted from their relative proportion in the total flora. Other studies have reported a similar association between dioecy and reduced flower size (Bawa, 1980; Ibarra-Manriquez and Oyama, 1992; Renner and Ricklefs, 1995; Chen and Li, 2008; Senarath, 2008; Vary et al., 2011; Schlessman et al., 2014). For example, dioecy was significantly associated with flower size less than 1 cm in the flora of the littoral forest of Madagascar (Vary et al., 2011). Reduced, inconspicuous flowers are generally associated with generalized pollination systems (Chen and Li, 2008). Generalized pollination system may provide a greater fitness advantage for small male flowers producing larger amounts of pollen, compared to that of few, large male flowers. In addition, many generalist pollinators may increase the transfer of pollen, as compared to specialized ones when the food rewards are similar across a number of plant species and when travel from plant to plant is costly (Waser et. al., 1996). Hence, a pollinator can generalize by including multiple flowering species in its foraging path collecting maximum resources with limited travel time. In addition, generalization may be favored when the availability of even the most effective pollinator is unpredictable from year-to-year (Johnson and Steiner, 2000). To further examine flower size in relation to pollination, a

comparison between features of dioecous and self-incompatible hermaphroditic species, such as number of flowers, pollen deposition rates, and seed quantities.

Many studies have shown an association between dioecy and seed dispersal attributes, which include fruit type and seed number (Bawa, 1980; Givnish, 1980; Flores and Schemske, 1984; Ibarra-Manriquez and Oyama, 1992; Renner and Ricklefs, 1995; Matallana et al., 2005; Senarath, 2008; Vary et al., 2011; Schlessman et al., 2014; Caruso et al., 2016). In this study, dioecious species more frequently had fleshy fruit than expected based on relative proportion of fleshy fruits in the total population. In addition, the one seeded fruits were more common than many seeded fruits in our flora. The incidence of fleshy fruit may be influenced by the frequency of woody habit in the tropics (Bawa, 1980). The predominance of animal dispersal (e.g., birds) in the tropics may also favor the fleshy fruit and few seeded traits. Seed number in this study was observed independently from fruit type due to further understanding the advantages seeds provide for seed dispersal (Ibarra-Manriquez and Oyama, 1992), which is essential for reproduction of plants. Animal dispersal of seeds is mainly accomplished by birds in the tropical regions, as compared to the temperate regions (Bawa, 1980; Givnish, 1980; Bawa et al., 1985). Birds rely on the fleshy fruit as a food source of woody plants in the tropics, favoring animal seed-dispersal (Bawa 1980; Givnish, 1980; Ibarra-Manriquez and Oyama, 1992; Vamosi and Vamosi, 2004; Matallana et al., 2005; Queenborough et al., 2007; Senarath, 2008), and seeds are dispersed by specialized frugivores, resulting in “high quality” dispersal. In seed-dispersal, birds also provide an advantage for seeds to travel a further distance more frequently, and often disperse around more sex-separated selected female species (Bawa, 1980; Givnish, 1980; Vamosi and Vamosi, 2004; Matallana et al., 2005; Senarath, 2008; Vary et al., 2011; Schlessman, 2014). This all influences an increase in plant fitness for female flowers of

dioecious species in the tropics, with more available resources devoted to fruit and seed production compared to hermaphroditic species (Bawa 1980; Givnish, 1980; Vamosi and Vamosi, 2004; Matallana et al., 2005; Queenborough et al., 2007). To further examine the association of seed dispersal, comparisons in dispersal rates between dioecious and self-incompatible hermaphroditic species may be examined.

In summary, the flora of the tropical premontane wet forest at Los Cusingos shows associations between dioecy and 1) woody growth (i.e., the long lived, perennial growth form), 2) flower size (i.e., tiny, inconspicuous, flowers pollinated by generalized, non-specific pollinators), and 3) fruit and seed characteristics (i.e., fleshy, single-seeded fruits that are often dispersed by specialized frugivores, resulting in “high quality” dispersal). Our findings support the premise that dioecy should be considered more than a mechanism to promote outcrossing. Dioecy is more likely a response to resource allocation (i.e., enhancement of male and female function) and spatial distribution of resource during pollination and seed dispersal.

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Table 1. Observed and expected number of species showing the associations between sexual systems and the ecological features (growth form, flower size, seed number, and fruit type) of the flora at Los Cusingos, Costa Rica.

		Sexual System								
		Hermaphroditic			Monoecious			Dioecious		
Feature	Total # Species	Observed	Expected	X^2	Observed	Expected	X^2	Observed	Expected	X^2
Growth Form										
Tree	116	73 (63%) ^a	84.9	1.72	19 (16%)	15.2	6.01	24 (21%)	15.9	8.53*
Shrub	110	89 (81%)	80.5		7 (6%)	14.2		14 (13%)	15.1	
Vine	59	44 (75%)	43.2		10 (17%)	7.7		5 (8%)	8.1	
Herb	28	23 (82%)	20.5		5 (18%)	3.7		0 (0%)	3.9	
				$P = 0.64$	$P = 0.11$				$P = 0.03$	
Flower Size										
Tiny	196	127 (65%)	143.4	2.96	33 (17%)	25.7	6.85	36 (18%)	26.9	7.37*
Small	79	68 (86%)	57.8		5 (6%)	10.4		6 (8%)	10.9	
Medium	19	18 (95%)	13.9		0 (0%)	2.5		1 (5%)	2.6	
Large	19	16 (84%)	13.9		3 (16%)	2.5		0 (0%)	2.6	
				$P = 0.40$	$P = 0.06$				$P = 0.04$	
Seed Number										
1-seeded	117	64 (55%)	85.6	5.30*	24 (21%)	15.3	6.61*	29 (25%)	16.1	13.82*
Many-seeded	196	165 (84%)	143.4		17 (9%)	25.7		14 (7%)	26.9	
				$P = 0.03$	$P = 0.01$				$P < 0.001$	
Fruit Type										
Fleshy	199	139 (70%)	145.6	0.47	23 (12%)	26.1	0.91	37 (19%)	27.3	9.18*
Dry	114	90 (79%)	83.4		18 (16%)	14.9		6 (5%)	15.6	
				$P = 0.53$	$P = 0.39$				$P = 0.003$	

^a Percentages in parentheses indicates the proportion out of total species in flora for each corresponding ecological feature.

* X^2 values with a asterisk are significant at $P < 0.05$.

Table 2. Observed and expected number of genera showing the associations between sexual systems and the ecological features (growth form, flower size, seed number, and fruit type) of the flora at Los Cusingos, Costa Rica.

Feature	Total # Genera	Sexual System									
		Hermaphroditic			Monoecious			Dioecious			
		Observed	Expected	X^2	Observed	Expected	X^2	Observed	Expected	X^2	
Growth Habit											
Tree	83	54 (65%) ^a	60.8	0.80	10 (12%)	9.3	2.17	19 (23%)	12.9	5.90	
Shrub	64	50 (78%)	46.9		5 (8%)	7.2		9 (14%)	9.9		
Vine	40	32 (80%)	29.3		4 (10%)	4.5		4 (10%)	6.2		
Herb	19	15 (79%)	13.9		4 (21%)	2.1		0 (0%)	3.0		
				$P = 0.86$					$P = 0.54$	$P = 0.11$	
Flower Size											
Tiny	118	74 (63%)	86.2	2.45	17 (14%)	13.3	3.24	27 (23%)	18.5	7.66*	
Small	55	47 (85%)	40.2		4 (7%)	6.2		4 (7%)	8.6		
Medium	17	16 (94%)	12.4		0 (0%)	1.9		1 (6%)	2.7		
Large	14	12 (86%)	10.2		2 (14%)	1.6		0 (0%)	2.2		
				$P = 0.49$					$P = 0.34$	$P = 0.04$	
Seed Number											
1-seeded	79	44 (56%)	57.5	3.04	12 (15%)	8.9	1.55	23 (29%)	12.6	11.05*	
Many-seeded	134	111 (83%)	97.5		12 (9%)	15.1		11 (8%)	21.4		
				$P = 0.09$					$P = 0.27$	$P = 0.001$	
Fruit Type											
Fleshy	124	80 (65%)	90.8	1.75	15 (12%)	14.0	0.16	29 (23%)	19.2	11.65*	
Dry	89	76 (85%)	65.2		9 (10%)	10.0		4 (4%)	13.8		
				$P = 0.20$					$P = 0.83$	$P = 0.001$	

^a Percentages in parentheses indicates the proportion out of total species in flora for each corresponding ecological feature.

* X^2 values with a asterisk are significant at $P < 0.05$.

Table 3. Frequencies of sexual system of global native angiosperm flora in different tropical regions

Geographical Region	Total Species	Hermaphroditic	Monoecious	Dioecious
Los Cusingos, Costa Rica (this study)	313	73.2%	13.1%	13.7%
Central Sarawak, Malaysia (Ashton, 1969)	711	60.0%	14.0%	26.0%
Puerto Rico and Virgin Islands (Flores and Schemske, 1984)	2037	78.9%	10.5%	6.1%
La Selva, Costa Rica (Bawa et al., 1985)	333	65.5%	11.4%	23.1%
Mexico (Bullock, 1985)	708	70.2%	13.0%	12.3%
Los Tuxtlas, Mexico (Ibarra-Manriquez and Oyama, 1992)	139	63.0%	9.0%	27.0%
Northern Australia (Gross, 2005)	1100	59.9%	22.1%	16.8%
Brazil (Matallana et al., 2005)	566	75.0%	11.0%	14.0%
China (Chen and Li, 2008)	685	60.6%	14.3%	25.1%
Sri Lanka (Senarath, 2008)	3529	79.1%	10.3%	7.1%
Taiwan and Orchid Island (Tseng et al., 2008)	3052	74.4%	11.1%	7.9%
New Caledonia (Schlessman et al., 2014)	3047	61.2%	12.8%	21.0%

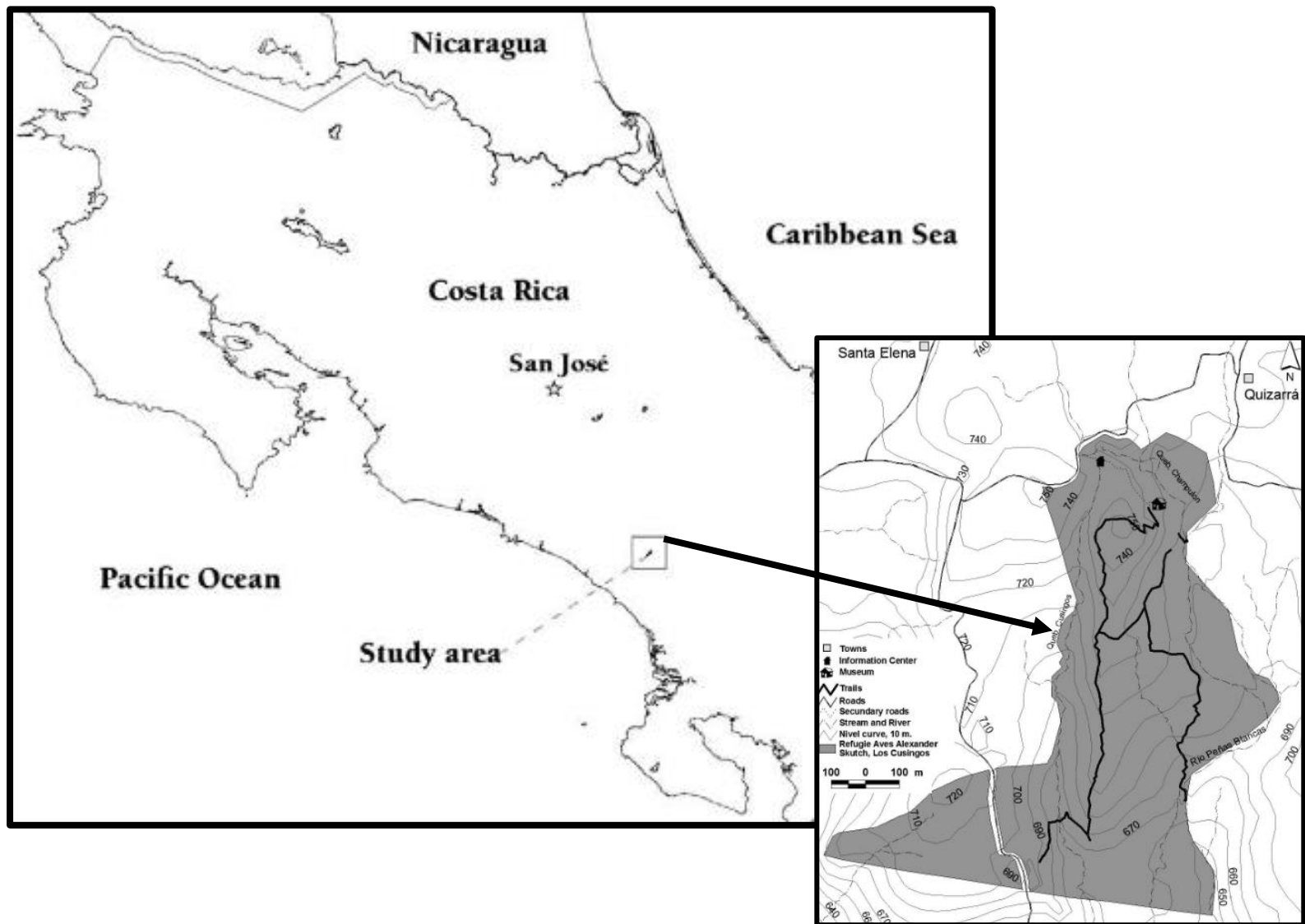


Figure 1. Map of Refugio de Aves Dr. Alexander Skutch, “Los Cusingos”, Costa Rica. This is the study site where first comprehensive botanical study and survey took place for collection and analysis of Costa Rican flora.

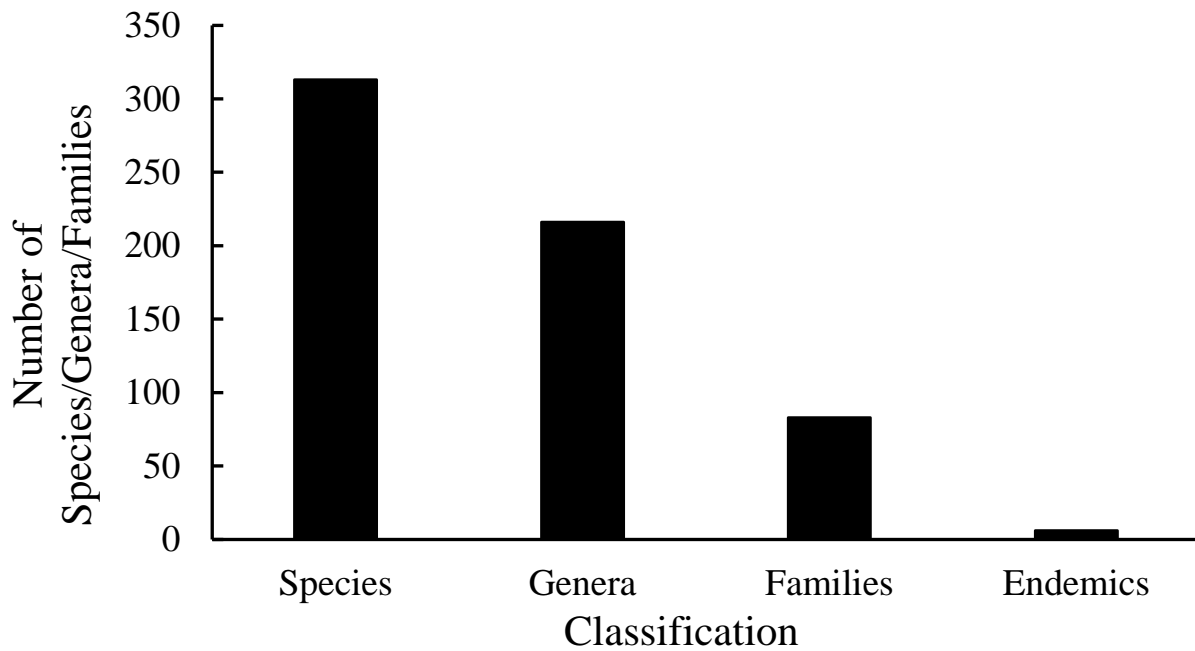


Figure 2. Summary of the taxa in the flora of tropical premontane wet forest in Costa Rica. The bars represent the number of species, genera, or families found in total flora. The number of endemics were recorded as the number of native species in the flora.

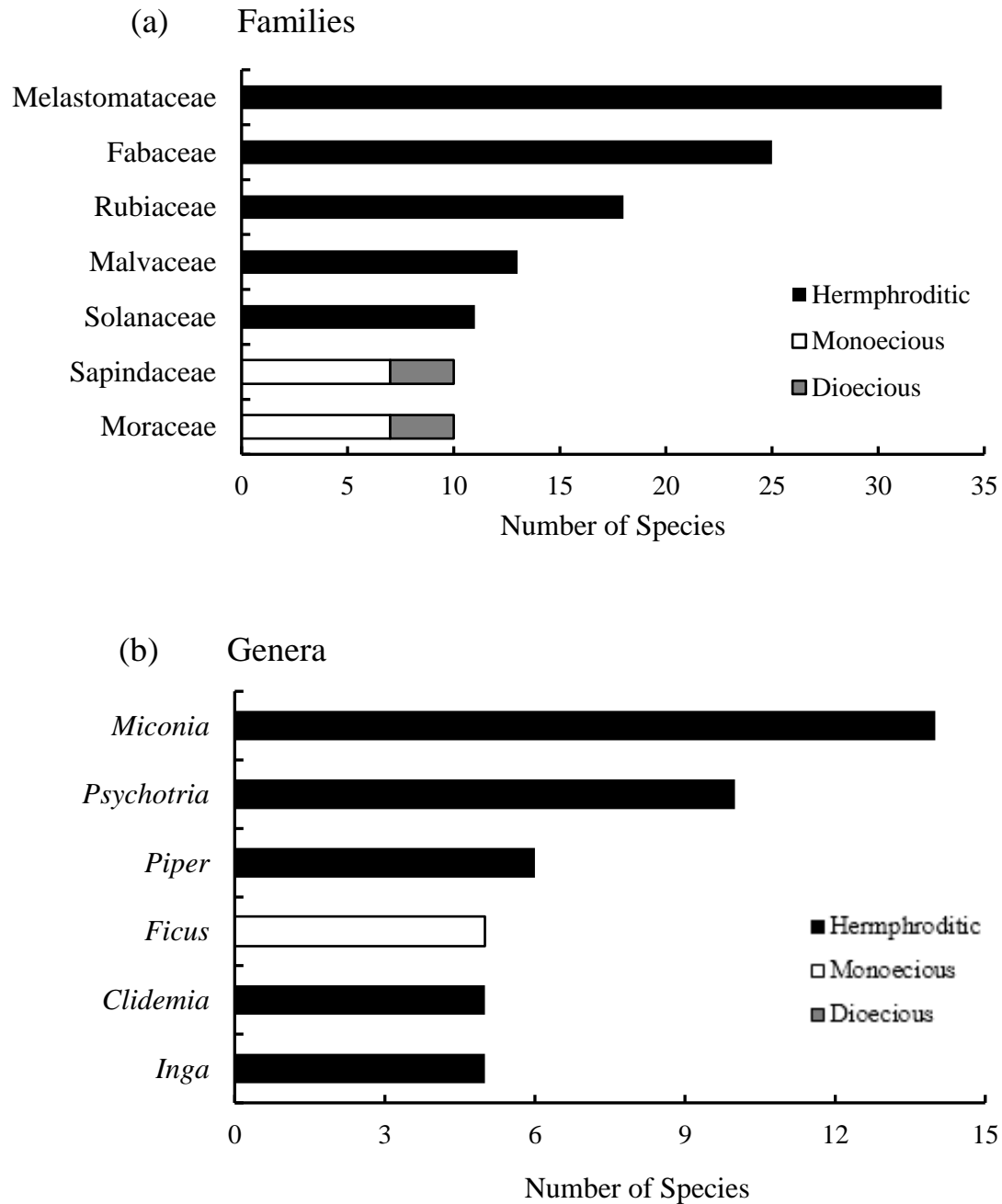


Figure 3. The frequency and sexual system of common taxa in the flora of a tropical premontane wet forest in Costa Rica. **(a)** 7 most abundant families comprised of 119 species or 38.0% of entire flora. **(b)** The 6 most abundant genera comprised of 45 species or 14.4% of entire flora.

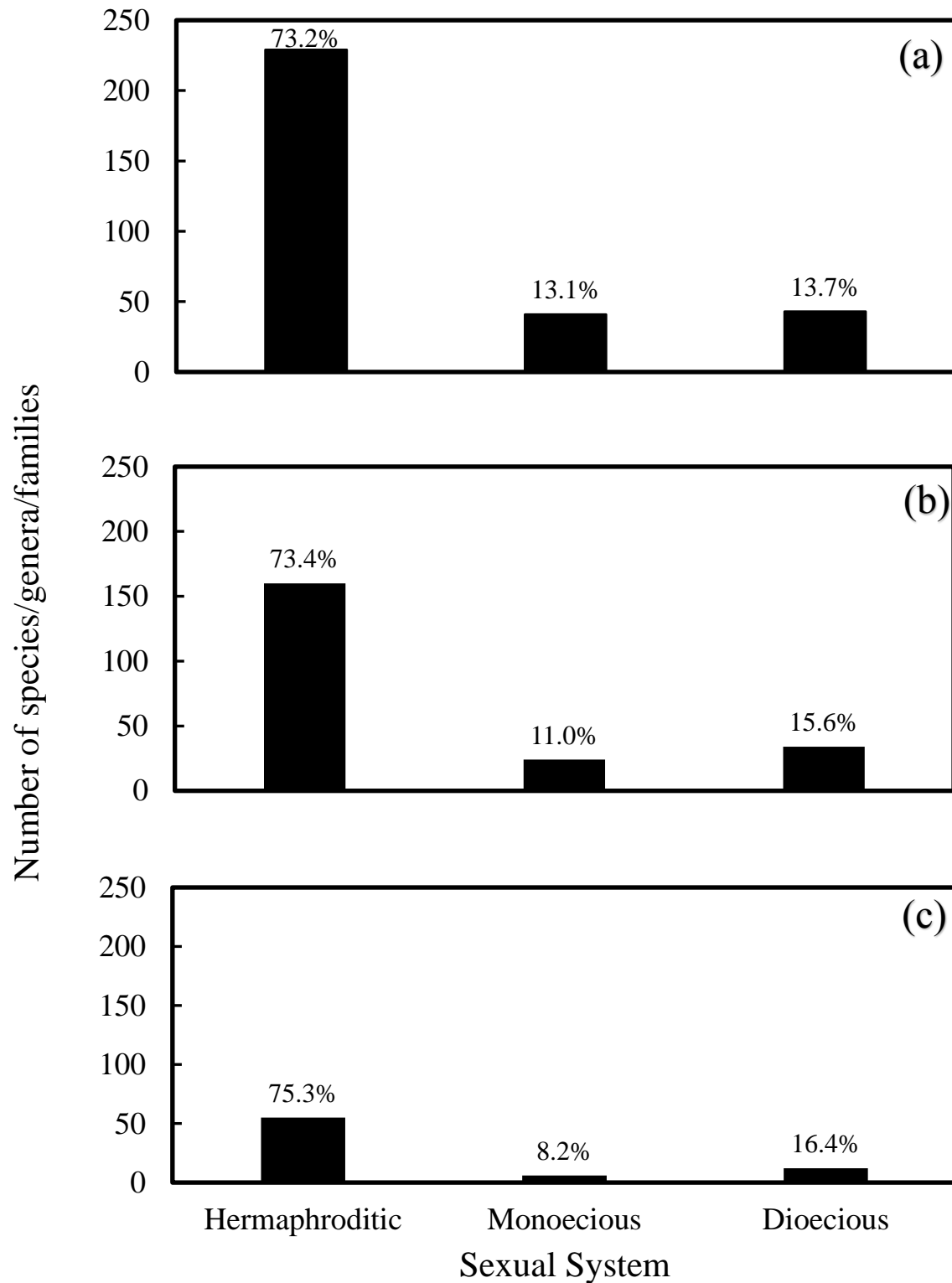


Figure 4. Abundance and sexual system of (a) species, (b) genera, and (c) families in the flora of a tropical premontane wet forest in Costa Rica.

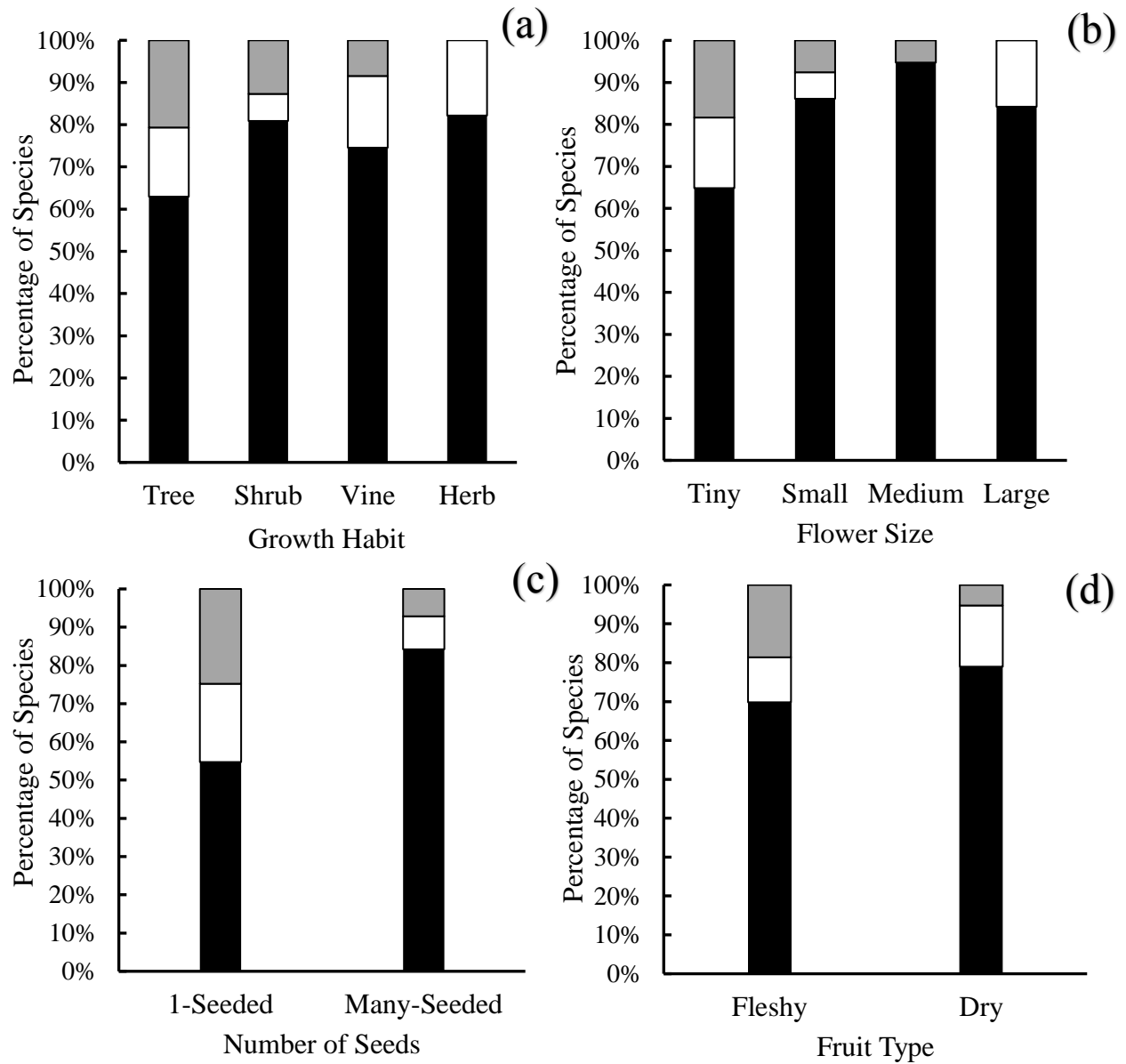


Figure 5. Percentage of hermaphroditic (black), monoecious (white), and dioecious (gray) species for **(a)** growth habit, **(b)** flower size, **(c)** seed number, and **(d)** fruit type in the flora of a tropical premontane wet forest in Costa Rica.. The total number of species was 313.

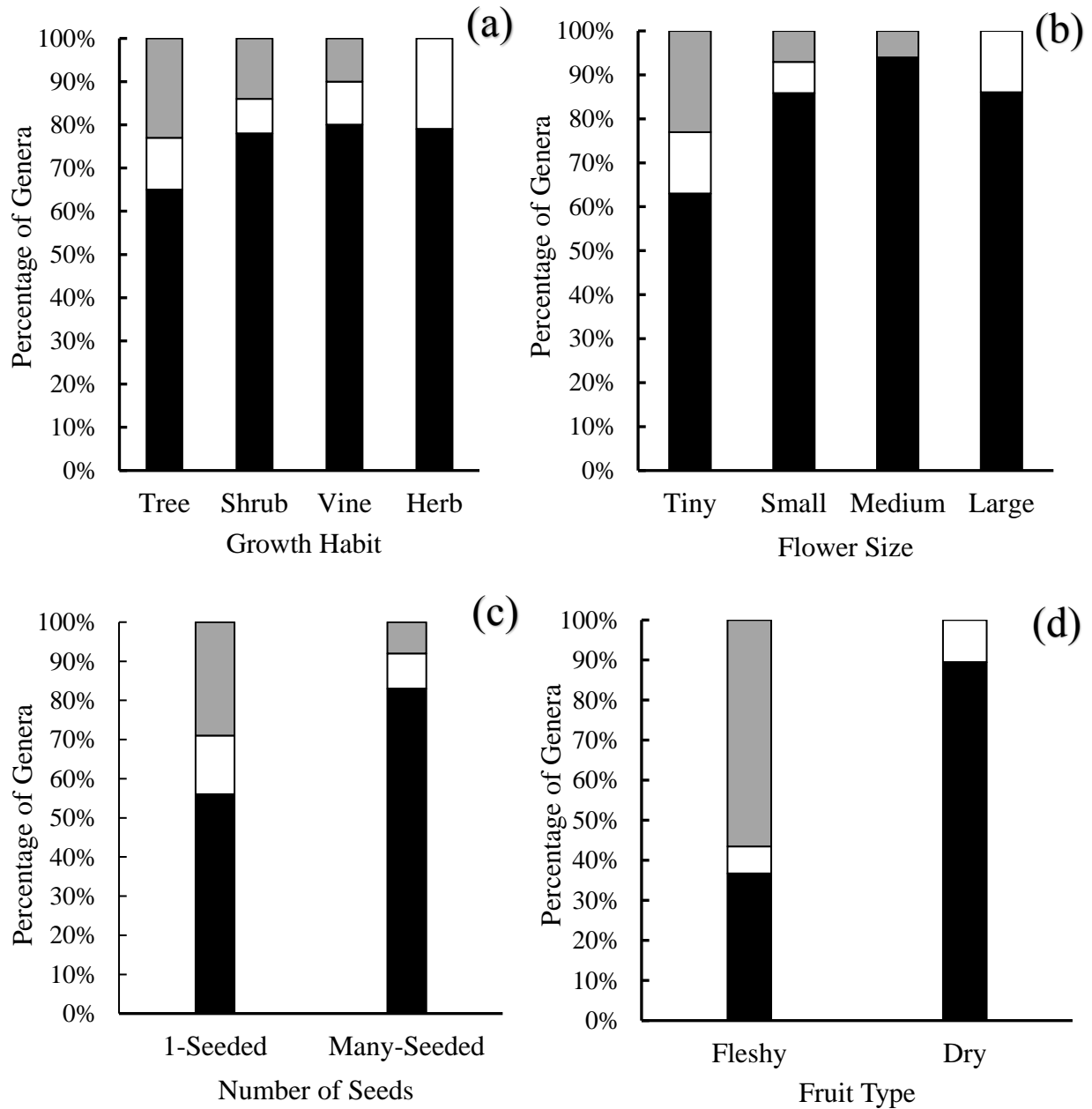


Figure 6. Percentage of hermaphroditic (black), monoecious (white), and dioecious (gray) genera for (a) growth habit (out of 206 genera), (b) flower size (out of 204 genera), (c) seed number (out of 213 genera), and (d) fruit type (out of 213 genera) in the flora of a tropical premontane wet forest in Costa Rica..

Appendix I

The following is a list of all 313 species included in this study. All species are native and angiosperms of Costa Rica recorded in Los Cusingos and adapted from Jones et al. (2015).

Acanthaceae

Aphelandra golfoducensis
Mendoncia gracilis
Mendoncia lindavii
Odontomea tubaeforme
Poikilacanthus macranthus
Thunbergia erecta

Achariaceae

Lindackeria laurina

Actinidaceae

Saurauia montana

Anacardiaceae

Anacardium excelsum
Spondias radlkoferi

Annonaceae

Annona amazonica
Guatteria recurvisepala
Xylopia frutescens

Apocynaceae

Aspidiosperma spp.
Macroscepis hirsuta
Mandevilla hirsuta
Peltastes isthmicus
Prestonia portobellensis
Tabernaemontana donnell-smithii
Tabernaemontana pauli

Araceae

Anthurium scandens
Anthurium spp.
Monstera deliciosa
Dieffenbachia spp.
Dracontium gigas
Philodendron spp. 1
Philodendron spp. 2

Araliaceae

Dendropanax arboreus
Schefflera morototoni

Arecaceae

Bactris glandulosa
Bactris hondurensis
Chaemadorea tepejilote

Geonoma ferruginea
Geonoma pinnatifrons
Prestoea acuminata
Socratea exorrhiza
Euterpe precatoria

Aristolochiaceae

Aristolochia pilosa

Asteraceae

Eirmocephala brachiata
Hidalgoa ternata
Lasianthaea fruticosa
Mikania riparia
Piptocarpha poeppigiana
Piptocoma discolor
Zexmenia virgulta

Begoniaceae

Begonia multinervia

Bignoniaceae

Callichlamys latifolia
Crescentia cujete
Fridericia patellifera
Handroanthus ochraceus
Jacaranda copaia
Lundia corymbifera
Pleonotoma variabilis

Bixaceae

Bixa orellana

Boraginaceae

Cordia bicolor
Cordia curassavica
Tournefortia bicolor

Bromeliaceae

Aechnea spp.

Burseraceae

Protium ravenii
Protium tenuifolium
Tetragastris panamensis

Cactaceae

Epiphyllum phyllanthus
Weberocereus imitans

Calophyllaceae

Marila laxiflora

Campanulaceae

Centropogon granulosus

Cannabaceae

Celtis iguanaea
Trema micrantha

Caricaceae

Jacaratia dolichaula

Chysobalanaceae

Licania platypus

Clethraceae

Clethra lanata

Clusiaceae

Chrysochlamys glauca
Clusia croatii
Clusia uvitana
Garcinia intermedia
Symphonia globulifera
Tovomita weddelliana

Combretaceae

Buchenavia tetraphylla
Terminalia oblonga

Convolvulaceae

Jacquemontia ciliata
Maripa nicaraguensis

Costaceae

Costus guanaiensis
Costus scaber

Cucurbitaceae

Gurania coccinea
Sechium pittieri

Cyclanthaceae

Asplundia alata
Asplundia euryspatha
Carludovica drudei

Cyperaceae
Scleria secans

Dichapetalaceae
Dichapetalia brenesii

Dilleniaceae
Davilla kunthii

Elaeocarpaceae
Sloanea laurifolia

Ericaceae
Satyria panurensis

Erythroxylaceae
Erythroxylum citrifolium
Erythroxylum macrophyllum

Euphorbiaceae
Acalypha diversifolia
Acalypha macrostachya
Alchornea latifolia
Croton draco
Croton smithianus
Croton tenuicaudatus

Fabaceae
Albizia saman
Calliandra calyothyrsus
Calliandra riparia
Canavalia brasiliensis
Diphysa americana
Entada gigas
Enterolobium schomburgkii
Erythrina costaricensis
Erythrina fusca
Gliricidia sepium
Inga edulis
Inga oerstediana
Inga spectabilis
Inga thibaulidiana
Inga umbellifera
Machaerium kegelii
Machaerium seemannii
Mimosa myriadena
Mucuna holtonii
Platymiscum pinnatum
Senna spectabilis
Senna hayesiana
Stryphnodendron microstachyum
Swartzia costaricensis
Zygia longifolia

Gesneriaceae

Drymonia macrantha

Heliconiaceae
Heliconia irrasa
Heliconia danielsoniana

Humiriaceae
Humiriastrum diguense

Hypericaceae
Vismia baccifera
Vismia macrophylla

Lacistemataceae
Lacistema aggregatum

Lamiaceae
Cornutia pyramidata
Scutellaria costaricana

Lauraceae
Beilschmiedia tovarensis
Nectandra membranacea
Ocotea cernua
Ocotea laetevirens
Persea caerulea

Loganiaceae
Strychnos chlorantha
Strychnos panamensis

Loranthaceae
Psittacanthus scheideanus
Struthanthus leptostachyus
Struthanthus orbicularis

Lythraceae
Lafoensia punicifolia

Malpighiaceae
Banisteriopsis muricata
Byrsonima crassifolia
Stigmaphyllon puberum

Malvaceae
Abutilon purpusii
Ceiba pentandra
Goethalsia meiantha
Heliocarpus americanus
Hibiscus furcellatus
Malvaviscus penduliflorus
Pachira sessilis
Pachira aquatica
Pavonia dasypetala
Pseudobombax septenatum
Sida urens

Sterculia recordiana
Wissadula excelsior

Marantaceae
Calathea crotalifera

Marcgraviaceae
Souroubea vallicola

Melastomataceae
Aciotis indecora
Adelobotrys adscendens
Bellucia pentamera
Blakea gracilis
Clidemia capitellata
Clidemia dentata
Clidemia discolor
Clidemia hirta
Clidemia sericea
Conostegia subcrustulata
Conostegia superba
Graffenrieda galeottii
Henriettea succosa
Henriettella fascicularis
Leandra grandifolia
Miconia affinis
Miconia argentea
Miconia bubalina
Miconia chrysophylla
Miconia elata
Miconia gracilis
Miconia holosericea
Miconia lacera
Miconia matthaei
Miconia minutiflora
Miconia prasina
Miconia schlimii
Miconia serrulata
Miconia trinervia
Mouriri gleasoniana
Ossaea macrophylla
Tibouchina longifolia
Topobea maurofernandeziana

Meliaceae
Cedrela odorata
Trichilia pallida

Menispermaceae
Abuta panamensis
Cissampelos fasciculata
Cissampelos pareira
Odontocarya truncata

Monimiaceae
Mollinedia viridiflora

Moraceae

Brosimum guianense
Brosimum utile
Ficus brevibracteata
Ficus citrifolia
Ficus colubrinae
Ficus costaricana
Ficus tonduzii
Maquira guianensis
Sorocea trophoides

Myristicaceae

Compsonura excelsa
Virola sebifera
Virola surinamensis

Myrtaceae

Eugenia grayumii
Myrcia splendens
Myrciaria floribunda
Psidium guajava

Nyctaginaceae

Neea laetevirens
Neea psychotrioides

Orchidaceae

Brassia gireoudiana
Epidendron pseudepidendron
Gongora leucoxyla
Oncidium dichromaticum
Xylobium sulfurinum

Passifloraceae

Passiflora ambigua
Passiflora costaricensis
Passiflora quadrangularis
Passiflora vitifolia

Phytolaccaceae

Phytolacca rivinoides

Piperaceae

Piper aduncum
Piper arboreum
Piper auritum
Piper biseriatum
Piper corrugatum
Piper curtispicum

Poaceae

Chusquea simpliciflora
Lasiacis maculata
Lasiacis procerrima
Lasiacis rugelii

Lasiacis sorghoidea
Olyra latifolia

Polygalaceae

Securidaca diversifolia

Primulaceae

Ardisia opegrapha
Ardisia guianensis

Rhamnaceae

Gouania columbiana
Gouania lupuloides

Rubiaceae

Condaminea corymbosa
Hamelia patens
Palicourea guianensis
Palicourea tetragona
Palicourea triphylla
Psychotria aurantibractea
Psychotria berteriana
Psychotria deflexa
Psychotria elata
Psychotria gracilentia
Psychotria marginata
Psychotria microbotrys
Psychotria poeppigiana
Psychotria racemosa
Psychotria solitudinum
Rudgea cornifolia
Sabicea panamensis
Tocoyena pittieri

Salicaceae

Banara guianensis
Casearia sylvestris
Hasseltia floribunda

Santalaceae

Dendrophthora turrialbae
Phoradendron crassifolium

Sapindaceae

Allophylus psilospermus
Dilodendron costaricense
Dilodendron elegans
Paullinia alata
Paullinia brenesii
Paullinia faginea
Paullinia rugosa
Serjania caracasana
Serjania mexicana
Serjania rhombea

Sapotaceae

Pouteria durlandii
Pouteria torta

Schlegeliaceae

Schlegelia parviflora

Simaroubaceae

Simarouba amara

Siparunaceae

Siparuna gesnerioides
Siparuna guianensis
Siparuna thecaphora

Solanaceae

Acnistus arborescens
Brugmansia suaveolens
Cestrum racemosum
Juanulla mexicana
Lycianthes beckneriana
Lycianthes multiflora
Solanum circinatum
Solanum jamaicense
Solanum rugosum
Solanum schlechtendalium
Witheringia coccoloboides

Staphyleaceae

Turpinia occidentalis

Tiliaceae

Heliocarpus americana

Urticaceae

Cecropia obtusifolia
Cecropia peltata
Myriocarpa longipes
Pourouma bicolor

Verbenaceae

Citharexylum cooperi
Lantana camara

Vitaceae

Cissus brevipes
Cissus cacuminus
Cissus erosa
Cissus fuliginea

Vochysiaceae

Vochysia ferruginea
Vochysia guatemalensis