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Zygomorphic Flowers May Reduce Extinction Rates by Allowing Angiosperms to Occur in Low Abundances

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Abstract

The high species richness that angiosperm show has been extensively correlated with key floral innovations. Key floral traits contribute to species boundaries and the origin of new species. However, how these relate to extinction remains largely untested. Among the multiple theories that attribute diversification to floral innovations, the reduced extinction model predicts that floral specialization allows the persistence of small populations and avoids their loss. Bilateral symmetry (zygomorphy) is a trait that has evolved recurrently in angiosperms. It is a form of floral specialization that restricts pollination to fewer visitors and precisely places pollen to ensure more effective transmission of pollen between conspecific flowers. In this study, I investigate the relationship between floral symmetry and abundance of species from 33 (1 ha) plots in tropical and subtropical forest in the Madidi National Park, Bolivia. If zygomorphy reduces the extinction of rare species, that is, species with small local abundance and low occupancy then, zygomorphy is present in smaller and more dispersed populations. For this, I carry out linear models with phylogenetic correction that explain the abundance of 545 species according to zygomorphy of the petals, of the stamens and stigma, and corolla shape. Results show that corolla zygomorphy is present in species with smaller populations. Species that contribute to this pattern are mainly present in the species-rich sub-humid and humid forest. However, zygomorphy of the reproductive organs does not have a significant impact in species abundances except for the analysis of species from the higher elevation. Multiple selective forces can shape the abundance of species. When facing the biotic forces that affect success of reproduction, such as pollinator availability and interspecific pollination, zygomorphy seems to provide an advantage to species that are rare by allowing them to persist at low abundances. More studies that further explore the causes for zygomorphy in smaller populations and the extinction rate using phylogenetic methods can help to understand how species loss is avoided.

Key words: Zygomorphic, bilateral symmetry, abundance, rarity, pollination, extinction

INTRODUCTION

Angiosperms have diversified rapidly, and with variation among clades. Fossil records, morphometric and molecular phylogenetic studies (Sauquet et al., 2017) demonstrate that floral innovations and modifications of shape are correlated with accelerated diversification (Endress, 2011) because they confer evolutionary success to the lineages they evolve in (Armbruster, 2014; Hernández-Hernández & Wiens, 2020). Floral traits are innovations (Armbruster, 2014) that, through reproductive isolation (Betts et al., 2021; Neal et al., 1998; Stebbins, 1970) contribute to species boundaries and the origin of new species (Sargent, 2004; Schluter, 2001). Floral symmetry, corolla shape, nectar spurs, and stamen number and location are key innovations of the different organs and organ complexes of the flower (de Vos et al., 2014; Fernández-Mazuecos et al., 2019; Hileman, 2014; Neal et al., 1998; O'Meara et al., 2016; Sargent, 2004). Among them, zygomorphy or bilateral symmetry is thought to recurrently facilitate species diversification in highly diverse clades like the order Lamiales (Cubas, 2004), and the families Orchidaceae and Fabaceae (Endress, 2012; Reyes et al., 2016) as well as several less diverse families (Kalisz et 9al., 2006; Sargent, 2004; Sauquet et al., 2015).

The two main types of floral symmetry described in the angiosperms are zygomorphy (Fig.1B and 1C) and actinomorphy (Fig.1A) (Endress, 2011). Zygomorphy is observed when a single cut in the axis of symmetry of the flower results in two identical mirror-like halves. Actinomorphy or radial symmetry, on the other hand, is observed when multiple cuts along more than one axis of symmetry result in identical halves. Still, the description of zygomorphy throughout the literature varies (Sauquet et al., 2015) because it may affect the perianth, androecium, gynoecium, or any combination of these (Endress, 2012). Most commonly it is present in at least two ways: at the level of the corolla (petals) level, and/or the level of the androecium (stamens) and gynoecium (stigmas) (Endress, 2012; Reyes et al., 2016; Sargent, 2004). This decomposition helps to understand the functional importance of the zygomorphy of petals and/or stamens and stigmas to establish a specialized relationship with pollinators. For instance, the two ventral petals of a papilionoid legume flower are transformed into a landing platform for insect pollinators and display visual guides that lead them into the flower from a specific direction. Once the pollinator is inside the flower, the stamens may be reduced in certain positions, or clustered in one side to facilitate the access of the pollinator to the nectar and pollen (Cubas, 2004; de Vos et al., 2014).

Zygomorphy is key because it increases the specificity of the pollination process in two main ways. First, it aids in restricting the access of visitor to a subset of fewer pollinators (Muchhala, 2007; Yoder et al., 2020). Zygomorphic flowers are usually facing to the sides (Neal et al., 1998), which further guides pollinators in a specific and consistent direction (Endress, 2012; Fenster et al., 2009). The position of the flower to ensure reproduction success is so critical that they have typically evolved the ability to restore flowers to a proper orientation after mechanical accidents that misplace them (Armbruster & Muchhala, 2020). Second, zygomorphy enhances cross-pollination efficiency by precisely controlling the close contact of the stamens (pollen export) or the stigmas (pollen receipt) with the pollinator’s body (Cubas, 2004), typically to a specific area in the dorsal or ventral surfaces of the pollinator (Armbruster, 1998; Reyes et al., 2016; Sargent, 2004). For example, three species of zygomorphic Lobelia avoid interspecific pollination through a pollen pump mechanism that deposits pollen in three distinctive locations on their bat pollinators: then end of the snout, between the ears, and the middle of the forehead (Koch, 2006).

Zygomorphy can interact with other key floral traits, such as scent, color, and corolla shape, to further specialize on a particular type of pollen vectors (Fenster et al., 2004; O’Meara et al., 2016; Ollerton et al., 2009; Reyes et al., 2016). For instance, a tubular corolla can restrict nectar accessibility to animals with the correct length or shape of mouthparts (Chmel et al., 2021; Muchhala, 2006). By manipulating pollinator behavior to attract specific pollinators that have greater constancy during a foraging trip (Yoder et al., 2020), such floral adaptations ultimately enhance pollinator effectiveness (Armbruster, 2014; Fenster et al., 2004). Indeed, a recent metanalysis of 2700 angiosperm species showed that zygomorphic species have fewer species of visitors, and share more of these visitors (i.e., potential pollinators) with other zygomorphic species than with other actinomorphic species (Yoder et al., 2020).

Through this effect in reproduction, floral specialization can contribute to maintaining species boundaries and increasing species richness within plant clades. It is widely accepted that pollinator-mediated reproductive isolation can generate genetic isolation accelerating speciation (Grant, 1984; Reyes et al., 2016; Stebbins, 1970). This can be readily seen in highly specialized pollinator systems, such as those of orchids. However, floral traits may not be always a sufficient barrier (floral isolation sensu stricto as in Armbruster, 2014) for species to genetically diverge without an initial postzygotic barrier (Armbrus99ter & Muchhala, 2009). But more frequently, the isolation produced by floral traits may be just enough (sensu lato) to reduce interspecific pollinator competition (Moreira-Hernández & Muchhala, 2019) and increase reproductive success (Fenster et al., 2004). The first is a mechanism that allows the coexistence of more species in sympatry. The latter increases the probability of success of conspecific pollen transmission and fertilization. Thus, these species may be more resilient to spatial, climatic, or pollinator availability disturbances that disrupt their normal rate of reproduction (McGill et al., 2007), to the point of reducing the risk of extinction. In consequence, floral specialization is more likely to contribute to species richness not through rapid speciation but by slowing down species loss (Armbruster & Muchhala, 2009).

In the case of zygomorphy, there are caveats on which process, extinction or speciation, is more important to explain species richness (Armbruster, 2014). Many authors suggest that specialized plants such as zygomorphic ones are at a greater risk of extinction during periods of pollinator scarcity or loss (Bergamo et al., 2020; Bevill & Louda, 1999; Sauquet, 2021; Yoder et al., 2020). However, this idea is contradicted by the strong correlation between zygomorphy and species richness (O'Meara et al., 2016; Sargent, 2004), it is a recurrent trait (Cubas, 2004; Endress, 2012) that has originated at least 130 (Sargent, 2004) to 154 times among angiosperms (Joly & Schoen, 2021). These observations are more consistent with a reduction in species extinction owing to the evolution of zygomorphic flowers (Armbruster & Muchhala, 2009). As described before, zygomorphy aids to reproductive success and confers resilience to disturbances. Both are key features in small populations that are at a greater risk of extinction during disturbances that decimate their already scarce number (Gaston, 1994; Vermeij &

Grosberg, 2018). In small populations, there is lower availability of plants and pollen; thus, fewer individuals can contribute to reproduction, but the effectiveness of this reproduction with zygomorphy is adequate for population growth and to sustain a viable population. Pollen limitation affects fitness at a lower threshold of population density. In other words, small populations that present zygomorphy can persist below a critical number of individuals at which the population growth of non-specialized species drops and leads to extinction (Fig.2).

One prediction the reduction of extinction hypothesis makes is that zygomorphic species will be able to occur in lower abundances than actinomorphic species. Put another way, rare species (those with lower number of individuals or population density; Rabinowitz, 1981) with actinomorphic flowers will be more likely to go extinct than rare species with zygomorphic flowers, leading to an accumulation of zygomorphic species with low abundances. In support of this idea, Harper (1979) observed an overrepresentation of floral zygomorphy among rare species of herbs. To provide a novel test of this extinction model, in this study I assess the relationship between floral symmetry and abundance for 545 tree species from the tropical Andean forest in the Madidi National Park in Bolivia. I did a model regression between the abundance of zygomorphic and non-zygomorphic species with a phylogenetic non-independence correction. Results support the prediction, in that zygomorphic species have significantly lower abundances than non-zygomorphic species, consistent with the hypothesis that the observed association between zygomorphy and increased species richness is due to decreased extinction risk among zygomorphic species.

METHODS

Forest plot data

I use floristic data from the Madidi Project, a long-term collaboration between the Herbario Nacional de Bolivia, the Missouri Botanical Garden, and various other institutions and researchers (www.madidiproject.weebly.com). Specifically, the data from 33 forest plots located along a wide altitudinal gradient, ranging in elevation between 650 to 3400 m, in the Madidi National Park in La Paz, Bolivia. Each forest plot is 1-ha in total area. In these, all individuals of woody plant species (i.e., trees) with a diameter at breast height (DBH) ≥ 10 cm have been tagged, identified, and mapped. In total, the dataset includes information for 25,569 individuals. Of these, 90.6% are identified to a valid species name, and the rest are assigned to a morphospecies. All taxonomic work has been standardized across plots, and herbarium specimens have been collected to document each species and morphospecies in each site. These specimens are deposited at the Herbario Nacional de Bolivia and the Missouri Botanical Garden.

We divided our dataset by forest plot along the elevational gradient into three groups (Fig.3): (a) dry forest, (b) sub-humid and humid forest, and (c) upper montane forest. The dry forest (< 1200 m in elevation) is defined by a relatively low number of species (average of 51 spp/plot), marked seasonality and precipitation, and a floristic composition predominantly formed by species from the Fabaceae, Meliaceae, Bignoniaceae, Myrtaceae, Rubiaceae and Euphorbiaceae families. At the opposite extreme of the gradient, the upper montane forest (over 2300 m) is defined according to the elevation and average number of species (41 spp/plot) which mainly belong to the families Lauraceae, Asteraceae, Melastomataceae, and Rubiaceae. In between these two forest types, the sub-humid and humid forest contains the highest tree density (55 trees/0.1 ha), average number of species (97 spp/plot), and floristic diversity (dominated by Ericaceae, Fabaceae, Moraceae, Lauraceae, Sapotaceae, Melastomataceae, Areaceae, Rubiaceae and Euphorbiaceae species). All statistical analyses were repeated for each forest type to account for the heterogeneity in environmental and biotic conditions among sites.

Abundance metrics

A species abundance can be characterized in multiple different ways and across spatial scales, each metric with potentially different biological interpretations. Therefore, the use of different abundance metrics is often necessary to fully depict commonness or rarity within an assemblage or landscape (Bock & Ricklefs, 1983). Local abundance and regional distribution are two common ways to characterize the abundance of a species at the local community and regional scale, respectively (Brown, 1984; Gaston, 2010; He & Gaston, 2003). Species can be characterized according to where they fall along these two dimensions of variation. Thus, I calculate the abundance at local scale, and occupancy at a broader scale (Fig. 4). The local abundance is the average number of individuals of a species in all the plots the species is present. It provides the average frequency of individuals of a species located within an area of the size of a plot (1 ha). The occupancy is the number of plots in which a species occurs. It represents the proportion of all the sites that contain at least one individual of a species in the region of study.

Floral trait data

I assembled a database of floral traits for 545 tree species. The floral traits are binary categorizations (yes or no) of corolla symmetry (zygomorphic), reproductive organs symmetry (zygomorphic), and corolla fusion (tubular). I included a fourth binary categorization of specialized or not, where a flower is specialized if it possesses at least one of the three traits (any of the two types of zygomorphy or a tubular corolla).

Because zygomorphy depends on the many parts that form the ground plan of a flower (Sauquet et al., 2015), I separated zygomorphy of a flower in two traits that functionally affect pollination: zygomorphy of the petals (corolla symmetry), and zygomorphy of the androecium and gynoecium (reproductive organs symmetry). A floral corolla is zygomorphic when it presents a slight to strict bilateral symmetry (Fig. 1B and 1C) and is not when it has more than one axis of symmetry, such as actinomorphic (Fig. 1A), asymmetric, dissymmetric, or other form of symmetry (Reyes et al., 2016; Sauquet et al., 2015). The zygomorphy of the corolla is determined for the petals, or when other parts of the perianth (e.g., sepals) perform as petals and affect the access of visitors to the flower. Flowers without petals were classified as non-zygomorphic. For inflorescences that mimic a solitary flower (i.e., blossoms; Armbruster, 1998), the symmetry is defined for the blossom. The reproductive organ symmetry is zygomorphic when the distribution of the stamens or stigmas is symmetrical in a single plane to the perianth (Kalisz et al., 2006). Only functional stamens in hermaphrodite or male flowers are considered for this classification (i.e., not staminodes) (O'Meara et al., 2016). The most common form of zygomorphic reproductive organ position is when all stamens are located on one side (Fig.1C) (e.g., Melastomataceae). Another form is when the style starts from anywhere but the middle of the ovary, positioning the stigma away from the center of the flower (e.g., Chrysobalanaceae).

I classify corolla as tubular when at least 1/3 of the total length of the petals is fused at anthesis. For species that present a superior ovary, the petal fusion is considered above the floral cup or hypanthium limit (Sauquet et al., 2015).

The floral traits were collected from online photos and descriptions from identification webpages such as Tropicos (http://legacy.tropicos.org/Home.aspx), NY virtual herbarium (http://sweetgum.nybg.org/science/vh/), The Plant List (http://www.theplantlist.org/tpl1.1/record/kew-200661), iNaturalist (https://www.inaturalist.org/), plant illustrations (http://plantillustrations.org/), Field Museum (https://collections-botany.fieldmuseum.org/), Encyclopedia of life (https://eol.org/), GBIF Global Biodiversity Information Facility (https://www.gbif.org/), Biodiversity Heritage Library (https://www.biodiversitylibrary.org/) and The phylogeny of Angiosperms (http://angio.bergianska.se/). I provide the links to each species sources used to obtain the trait data in the assembled database. To help with the classification of species that had no photos available online, I used the descriptions from Rudas Lleras et al., (2005) and Steyermark et al., (1995).

Abundance comparisons between floral traits and floral specialization

To compare the species abundances between floral trait states (e.g., yes=1 vs. no=0 for corolla symmetry), I carried out ordinary least squares (OLS) regressions. This type of linear least squares method fits the data in a linear regression model and assumes independence of the residuals. For this, I used the lm() function in R. Each regression has a response variable that is a species abundance metric and a predictor variable that is a floral trait. In total I carried out 8 regressions, of which 4 had local abundance, and the 4 had occupancy as the response variables. Note that local abundance is a continuous variable, the occupancy is a discrete variable, and the floral traits are binary discrete variables. The abundance metrics were log-transformed to approximate a normal distribution.

To compare the species abundances between floral trait states and to account for phylogenetic signal, I carried out a series of phylogenetic generalized least-squares (PGLS; Harvey & Pagel, 1991) analyses. This approach incorporates the probability that closely related species tend to resemble each other (i.e., phylogenetic signal), and compensates for this non-independence effect by weighting the phylogenetic relationships between species (Cornwell & Nakagawa, 2017; Hamon, 2019). It accommodates an uncertainty measurement in the tips of a phylogenetic tree, and when scaled up to a regression analysis it shows if a relationship is significant after incorporating the phylogenetic signal (Felsenstein, 1985; Revell, 2010). This analysis corrects for the possibility of having closely related species that are likely to conserve similar floral trait values due to shared evolutionary history and affect the assumptions of the regression analysis (E-Vojtkó et al., 2020; Revell, 2009, 2010).

The PGLS accommodates residual errors based on a variance-covariance matrix that represents the expected covariance between species' trait values, given a phylogenetic tree and under a specific model of evolution (Revell, 2010). The expected covariance between species' trait values is proportional to the branch length of a species, the distance between the tip and the latest common ancestor, in a phylogenetic tree (Revell, 2009). Therefore, the trait values of a species consider the ancestral relationships between any pair of species in a tree. A phylogenetic tree for 545 species was generated using a backbone phylogeny from the package V.PhyloMaker (Jin & Qian, 2019), and the phylogeny developed for the Madidi Project by Linan et al., (in prep.) based on the mega-phylogeny for seed plants developed by Smith & Brown (2018).
I implemented the PGLS analyses using the function gls() from the R packages "nlme" (Pinheiro et al., 2013), and "phytools" (Paradis & Schliep, 2019). The generalized least squares (gls) regression allows the incorporation of the variance-covariance matrix

under a model of evolution. Among these, the Brownian motion (BM) model of evolution is typically used in phylogenetic analyses (Harmon, 2019). This model reflects a neutral evolution where continuous traits evolve according to a random process, so the branch lengths are expected to have a normal distribution (Garamszegi, 2014; Harmon, 2019; Revell, 2009). Whereas to mimic other evolutionary processes, branch length transformations can be used (e.g., Ornstein–Uhlenbeck, Pagel's λ) (Revell, 2009).

Results for a BM model of evolution are not reported because the binary discrete predictors violate the assumption of normal distribution of continuous traits of the BM model. Thus, I carried out the PGLSs using an Ornstein–Uhlenbeck (OU) model of evolution, which describes a BM model under the influence of friction (Martins & Hansen, 1997). The OU is different from the BM in that it assumes that the evolution of traits happens under natural selection and is adaptive, so evolution favors an optimum value (Butler & King, 2004; Garamszegi, 2014). This model applies better to the analysis of the binary predictors because it is testing if the state of a character is favored by selection. The pull of the evolution towards this single optimum value everywhere on the tree has the effect of transforming branch lengths, in the same way that Pagel's λ (Pagel, 1999) stretches a tree so that branch lengths better represent an evolutionary process (Garamszegi, 2014).

To compare between different models of evolution, I repeated the PGLSs using the branch transformation method Pagel's λ, which quantifies the strength of the phylogenetic relationships on trait evolution under a BM model (Blomberg & Garland, 2002; Freckleton, 2000). The λ metric varies between 0, when the phylogenetic signal is null, so the phylogenetic relationships do not explain the trait data, and the phylogenetic tree becomes a star phylogeny, and 1 when the phylogenetic relationships explain the trait data, and the traits change continuously and randomly through time (i.e., BM model) (Garamszegi, 2014; Harvey & Pagel, 1991). When λ takes any value between 0 to 1, the phylogenetic signal is intermediate and the PGLS can correct for phylogeny in the appropriate degree (Garamszegi, 2014). The λ value for the residuals of a model is calculated by the gls() function through Maximum Likelihood estimation.

I compared the PGLS analyses with OU and Pagel's λ methods with two functions from different R packages. The gls() from "nlme", and the function phylolm() from the R package "Phylolm" (Ho & Ané, 2014). Uncertainty of parameter estimates was estimated with bootstrap of 100 iterations. The results were identical with both packages, but Phylolm works faster with larger phylogenies. The OLS and PGLS (with OU and Pagel's λ) models were compared using the Akaike information criterion (AIC); the OU and Pagel's λ models outperformed the BM model, but both showed similar results. Therefore, I only report the PGLS results from the Pagel's λ method.

Because the hypothesis was tested multiple times for four floral traits x two abundance metrics (8 combinations), I implemented to every analysis with all species a Benjamini-Hochberg (BH) multiple test corrections with the p.adjust() function from the R package "FSA" (Raiche & Magis, 2020).

RESULTS

Floral trait groups

I analyzed 545 tree species of which 55 species present zygomorphic corolla, 88 species present zygomorphic reproductive organs, and 208 species present fused corolla. Floral specialization condenses all the species that had at least one specialized floral trait; 267 of the species present floral specialization. The distribution of the 545 species in the three types of forest include 117 species in dry forest, 406 species in sub-humid and humid forest, and 129 species in upper montane forest (Fig.5A). For all species and each forest type, approximately half of the species presented floral specialization, that is, presented one to three of the specialized floral traits (Fig.5B) (zygomorphic corolla [ZC], zygomorphic reproductive organs [ZRO], and fused corolla [FC]). A fused corolla is more common, followed by zygomorphic reproductive organs, and at last, by zygomorphic corolla (Fig. 5C). The zygomorphic species contributed to 10% of all the species, 14% of the dry forest species, 9% of the sub-humid and humid forest species, and 9% of the upper montane species.

I constructed a phylogeny for the 545 species which shows that zygomorphic corollas are distributed in six major clades (Fig.6). The clades differ in the number of zygomorphic species: Lamiales formed by eleven species from the families Lamiaceae, Verbenaceae and Bignoniaceae; Asteraceae formed by six species; Proteales formed by six species from the families Sabiaceae and Proteaceae; Sapindaceae formed by four species; Malpighiaceae formed by seven species; and Fabaceae formed by 13 species from the subfamilies Caesalpinoideae and Faboideae. Additionally, zygomorphic corollas are dispersed in aggregations of less than four species that belong to Ericaceae, Siparunaceae, Vochysiaceae and Euphorbiaceae.

In the case of zygomorphic reproductive organs, species are clustered in the same six clades of zygomorphic corolla plus three more (Fig.6) as follows: Melastomataceae formed by 29 species from the genus Miconia, Urticaceae formed by seven species from the genus Urera, and Moraceae formed by eight species from the genus Ficus. Additionally, the zygomorphic reproductive organs trait is dispersed in aggregations of less than four species that belong to Lecythidaceae, Rubiaceae, Vochysiaceae, Ochnaceae and Meliaceae.

Abundance comparisons between floral traits and floral specialization

There is an observable difference in the local abundance and occupancy between species with zygomorphic and non-zygomorphic corolla (Fig.7), and zygomorphic and non-zygomorphic reproductive organs (Fig.8). However, the contrasts between tubular and free corolla (Fig.9), and specialized and non-specialized flower (Fig.10) do not show differences.

To compare the abundance of species, I carried out OLS regressions for each floral trait across all species and each type of forest. The OLSs allows to determine if there is a statistically significant difference between the groups of study assuming that the variation of the predictor variable cannot be explained by the intrinsic correlation of phylogeny.

To correct for the probability that closely related species tend to share floral traits because of a common evolutionary history, I repeated the OLSs and did PGLS regressions using the branch transformation method Pagel's λ. The results of the OLSs in contrast to the PGLS models between floral traits and species abundance are shown for zygomorphic corolla (Table 1), zygomorphic reproductive organs (Table 2), tubular corolla (Table 3), and specialized flower (Table 4). Tubular corolla and specialized flower do not show significant results.

A significant statistical relationship between zygomorphy and abundance is supported by the ordinal and phylogenetic regressions for the all-species analysis and for the subset of species from sub-humid and humid forest analysis. Species with zygomorphic corollas have lower local abundance ($Ab_{ZYG} = 4.8$ vs. $Ab_{NON} = 10.1$, $\beta1 = -0.52$ [-0.95, -0.18], $p = 0.006$, R2 = 0.0137, n = 525 species) and lower occupancy ($Oc_{ZYG} = 2.0$ vs. $Oc_{NON} = 3.1$, $\beta1 = -0.39$ [-0.57, -0.17], $p = 0.0002$, R2 = 0.0244, n = 525 species) compared with non-zygomorphic species. Species from sub-humid and humid forest with zygomorphic corollas have lower local abundance ($Ab_{ZYG} = 2.5$ vs. $Ab_{NON} = 6.9$, $\beta1 = -0.51$ [-0.86, -0.15], $p = 0.012$, R2 = 0.015, n = 406 species) and lower occupancy ($Oc_{ZYG} = 1.3$ vs. $Oc_{NON} = 2.6$, $\beta1 = -0.50$ [-0.68, -0.34], $p = 0.00003$, R2 = 0.0427, n = 406 species) compared with non-zygomorphic species. Species from upper montane forest with zygomorphic reproductive organs have lower occupancy compared with non-zygomorphic species ($Oc_{ZYG} = 1.6$ vs. $Oc_{NON} = 2.5$, $\beta1 = -0.39$ [-0.66, -0.15], $p = 0.0052$, R2 = 0.0597, n = 129 species). The parameter estimates of the ordinal and phylogenetic regressions are in most cases identical, which is consistent with the close to 0 or weak phylogenetic signal (λ) of the variables' residuals in the PGLS results.

DISCUSSION

This study demonstrates that species with zygomorphic corollas occur at significantly lower abundances and occupancies than other species. This pattern can be the consequence of various mechanisms that shape species populations. Among the hypothesis proposed to understand diversity, the extinction reduction hypothesis (Armbruster & Muchhala, 2009) predicted this pattern through the effect of floral specialization.

The extinction reduction model hypothesizes that floral specialization reduces species extinction by diminishing interspecific pollination, and promotes tighter species packing in communities. Zygomorphy is a key floral trait that through pollinator specificity and pollination efficiency reduces interspecific pollinator competition and increases reproductive success. The first is a mechanism that allows the packing of more sympatric species. The latter increases the probability of success of conspecific pollen transmission and fertilization, so the reproduction of fewer individuals is efficient enough to sustain a viable population. Because of the improved reliability in reproduction, these populations are more resilient to spatial, climatic, or pollinator availability disturbances that may disrupt their normal rate of reproduction. In this way, floral specialization traits are expected to contribute to population persistence of rare species, that are at more risk of extinction. Altogether, the reduction of local extinction that promotes smaller or more dispersed populations of species allows the persistence of zygomorphic small populations.

Phylogenetic distribution of the floral traits

The zygomorphic species are found in six clades. Of these, Lamiales, Asteraceae, and Fabaceae have demonstrated an association of accelerated diversification with floral zygomorphy in previous studies (Cubas, 2004; Endress, 2012; Kalisz et al., 2006; Reyes et al., 2016; Sargent, 2004; Sauquet et al., 2015). In the case of the other major clusters Malphigiaceae, Sapindaceae and Proteales and the small ones Ericaceae, Vochysaceae, Euphorbiaceae and Siparunaceae the association has not been tested.

The six major clades are better represented in the sub-humid and humid forest; thus, this forest is the biggest contributor of zygomorphic species to the overall analysis. The humid forest hosts one of the highest numbers of species among tropical forest, indicating an average of 97 species per hectare in our database, of which rare species are predominant (Cornejo-Mejía et al., 2011). The zygomorphy in smaller population may be better represented in this type of forest because of a sample size effect of more zygomorphic species in the rich forest. The pattern may also be stronger here because the humid forest puts more competitive pressure on species so a trait like zygomorphy that reduces interspecific pollination and persistence, has more opportunity to evolve and be maintained in a diverse forest. In more extreme habitats like the dry forest and upper montane sites, perhaps pollen limitation imposes less of a selective pressure due to lower species richness and relatively stronger selection for growth/survival traits.

The phylogenetic distribution of the zygomorphic reproductive organs is similar to patterns for zygomorphic corollas, with the addition of the Melastomataceae, Moraceae, and Urticaceae clades. Each of these three clusters is formed by species from the same genus*: Miconia, Ficus* and *Urera*, respectively. *Miconia*'s buzz pollination by bees and *Ficus*'s pollination by mutualist wasps exhibit extreme pollinator specialization related to androecium modifications that are commonly associated to species diversification. The diversification of these two groups may be better explained by the models of rapid speciation because of extreme floral and pollinator specialization. This means that the extinction model does not significantly drive their diversification, thus our prediction of smaller or more dispersed populations would not apply to these genera.

There is no significant relationship between abundance and zygomorphic reproductive organs for the overall species and forest subsets analyses, except for the analysis for upper montane forest with occupancy. These results show that species with zygomorphic organs are restricted to fewer sites but do not have lower abundance locally. The upper montane forest extends from 2300 to 3000 m, where abiotic selective forces may drive community richness more than interspecific competition. At higher elevations, the lack of pollinator availability can intensify selection on floral specialization traits (Zhao & Wang, 2015). Corolla zygomorphy is an advantage for persistence at higher elevations in restricted and dispersed sites but because of climatic changes, the populations cannot persist in low densities.

Zygomorphy of reproductive organs is thought to be an intermediate step towards the evolution of full floral zygomorphy that includes the petals and/or sepals (Endress, 2012; Neal et al., 1998). It is a further step to precisely deposit pollen on specific pollinators (Fenster et al., 2009). This is only an intermediate step in the way to floral specialization but, reproductive organ zygomorphy alone may not provide enough pollinator specialization to allow the persistence of rare species and avoid their extinction.

Meliosma (cluster Proteaceae) and *Urera* (cluster Urticaceae) are genera with actinomorphic flowers that internally present zygomorphic stamens and stigmas, respectively, and use an explosive pollen release mechanism that instead of favoring pollinator specificity, favors pollination by wind and, in the case of *Meliosma*, discourages the visitation by pollen-harvesting bumblebee workers (Wong Sato & Kato, 2018). Explosive pollen dispersal is a common mechanism in zygomorphic tubular flowers (Wong Sato & Kato, 2018); this adaptation does neither restrict pollination to fewer visitors, nor does it not depend on the accurate match of pollen and stigma with the pollinator’s body. These two aspects are key in the floral specialization and reduction of extinction hypothesis. To my knowledge, there are no previous studies that have compared the levels or types of floral zygomorphy between species, and how they may affect their reproductive success.

Contrary to what was expected, tubular corollas were not significantly associated with species abundance. This may be due to the approach taken to characterize tubular corolla. This is a trait that is more accurately measured in length of the floral tube and width of the corolla (Fernández-Mazuecos et al., 2013), but this methodology was not applied because of the span of the study. This can also help explain why specialized flower, that integrates tubular flower, showed no relationship species abundance.

Zygomorphy and other floral specialization traits

The recurrent origin of a specific floral trait alone, such as zygomorphy does not necessarily confer evolutionary success over longer evolutionary timescales (de Vos et al., 2014; Fernández-Mazuecos et al., 2019). But zygomorphy may prompt the opportunity for flowers to reinvent themselves. The zygomorphy of flowers is a trait that has been well studied in dominant groups and has been described with other floral traits in floral syndromes. Some examples of other floral traits that act conjointly with zygomorphy to allow persistence of species are: a shorter length of flowering time for specific pollination evidenced in orchids pollinated by euglossine bees in central lowland Panama (Ackerman & Roubik, 2012), the pollen explosion dispersion mechanism of Meliosma (Wong Sato & Kato, 2018), the elongation of stamens for delayed self-fertilization evidenced in Crotalaria papilionoid flowers in South Africa (Veeresh Kumar et al., 2019), and the plastic production of cleistogamous or closed zygomorphic flowers for self-fertilization (Joly & Schoen, 2021). The latter is the most recent study with the largest database of floral symmetry.

Joly and Schoen (2021) hypothesized that cleistogamy is a form of phenotypical plasticity of flowers that allows self-fertilization through the close contact of stamens with stigmas when pollinators are scarce, and cross-pollination is not possible. They found a strong association between 828 zygomorphic species of which 15.2% are cleistogamous in comparison to 1,695 actinomorphic species of which only 3.2% are cleistogamous. It has been suggested that cleistogamy balances the increased risk of extinction of zygomorphic species during times of pollinator population fluctuation (Sauquet, 2021). To further understand this relationship, it would be interesting to do a finer-scale analysis of the abundance of zygomorphic species that present cleistogamy in comparison with zygomorphic species that do not present cleistogamy.

CONCLUSIONS

The increased likelihood of extinction due to low abundance does not always drive extinction of rare species; these rare species that are apparently in disadvantage have managed to persist over evolutionary times. Biodiverse communities are dominated by many rare species and few common species (McGill et al., 2007). Rare species possess traits that reduce their vulnerability to extinction during crisis; such an example may be zygomorphy that through the reduction of interspecific pollinator competition and insurance of reproduction success contributes to species persistence. The results show that zygomorphic species persist at lower abundances and occupancies in the Madidi forest, Bolivia. Because zygomorphy is a type of specialization that improves reliability in reproduction, it becomes a key trait in small populations, where there is lower availability of plants and pollen; so, fewer individuals can contribute to reproduction, but the effectiveness of this reproduction with zygomorphy is adequate for population growth and to sustain a viable population. In this way, floral specialization traits are expected to contribute to population persistence of rare species, leading to an accumulation of zygomorphic species with low abundances.

The fact that zygomorphic species occur at lower abundance supports the hypothesis that extinction reduction contribute to the documented association between floral specialization and increased diversification. This hypothesis is not as widely tested as others that involve speciation, and this study is one of the first to corroborate the prediction using a large database of tropical species.

To further test the extinction reduction hypothesis, it would be useful to directly test the extent to which zygomorphy reduces extinction. This is crucial to support the idea that zygomorphy is more common in rare species because it avoids their loss. Unfortunately, this is difficult to test using current phylogeny-based methods due to their limitations in detecting variation in extinction rates (Ackerman & Roubik, 2012). An alternative approach would be to use hand-crossing experiments to test the prediction that species with zygomorphic will be less pollen-limited than similar species with actinomorphic flowers.

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BIBLIOGRAPHY

Ackerman, J. D., & Roubik, D. W. (2012). Can extinction risk help explain plant-pollinator specificity among euglossine bee pollinated plants? Oikos, 121(11), 1821–1827. https://doi.org/10.1111/j.1600-0706.2011.20193.x

Armbruster, W. S. (1998). Multilevel Comparative Analysis of the Morphology, Function, and Evolution of Dalechampia Blossoms Author (s): W. Scott Armbruster Published by: Wiley Stable URL: http://www.jstor.org/stable/1941153 REFERENCES Linked references are available on JST. Ecology, 69(6), 1746–1761.

Armbruster, W. S. (2014). Floral specialization and angiosperm diversity: phenotypic divergence, fitness trade-offs and realized pollination accuracy. AoB PLANTS, 6, 1–24. https://doi.org/10.1093/aobpla/plu003

Armbruster, W. S., & Muchhala, N. (2009). Associations between floral specialization and species diversity: Cause, effect, or correlation? Evolutionary Ecology, 23(1), 159–179. https://doi.org/10.1007/s10682-008-9259-z

Armbruster, W. S., & Muchhala, N. (2020). Floral reorientation: the restoration of pollination accuracy after accidents. New Phytologist, 227(1), 232–243. https://doi.org/10.1111/nph.16482

Bergamo, P. J., Susin Streher, N., Traveset, A., Wolowski, M., & Sazima, M. (2020). Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. Ecology Letters, 23(1), 129–139. https://doi.org/10.1111/ele.13415

Betts, M. G., Hadley, A. S., Frey, D. W., Frey, S. J. K., Gannon, D., Harris, S. H., Kim, H., Kormann, U. G., Leimberger, K., Moriarty, K., Northrup, J. M., Phalan, B., Rousseau, J. S., Stokely, T. D., Valente, J. J., Wolf, C., & Zárrate-Charry, D. (2021). When are hypotheses useful in ecology and evolution? Ecology and Evolution, 00(1), ece3.7365. https://doi.org/10.1002/ece3.7365

Bevill, R. L., & Louda, S. M. (1999). Comparisons of Related Rare and Common

Species in the Study of Plant Rarity. Conservation Biology, 13(3), 493–498. https://doi.org/10.1046/j.1523-1739.1999.97369.x

Blomberg, S. P., & Garland, T. (2002). Tempo and mode in evolution: Phylogenetic inertia, adaptation and comparative methods. In Journal of Evolutionary Biology (Vol. 15, Issue 6, pp. 899–910). https://doi.org/10.1046/j.1420-9101.2002.00472.x

Bock, C. E., & Ricklefs, R. E. (1983). Range size and local abundance of some North American songbirds: a positive correlation. American Naturalist, 122(2), 295–299. https://doi.org/10.1086/284136

Brown, J. H. (1984). On the relationship beween abundance and distribution of species. American Naturalist, 124(2), 255–279. https://doi.org/10.1086/284267

Butler, & King. (2004). Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. The American Naturalist, 164(6), 683. https://doi.org/10.2307/3473229

Chmel, K., Ewome, F. L., Gómez, G. U., Klomberg, Y., Mertens, J. E. J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome is the plant’s adaptation to ornithophily, but nectarivorous birds are not so selective. Oikos, 1–14. https://doi.org/10.1111/oik.08052

Cornejo-Mejía, M., JØrgensen, P. P., Macía, M. M. J., Loza, I., Fuentes, A., & Cayola, L. (2011). Memorias de los 10 años de investigación botánica realizada en la Región Madidi: “conociendo una de las regiones más biodiversas del mundo.”

Cornwell, W., & Nakagawa, S. (2017). Phylogenetic comparative methods. In Current Biology (Vol. 27, Issue 9, pp. R333–R336). Cell Press. https://doi.org/10.1016/j.cub.2017.03.049

Cubas, P. (2004). Floral zygomorphy, the recurring evolution of a successful trait. BioEssays, 26(11), 1175–1184. https://doi.org/10.1002/bies.20119

de Vos, J. M., Hughes, C. E., Schneeweiss, G. M., Moore, B. R., & Conti, E. (2014).

Heterostyly accelerates diversification via reduced extinction in primroses. Proceedings of the Royal Society B: Biological Sciences, 281(1784), 20140075. https://doi.org/10.1098/rspb.2014.0075

E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., & Götzenberger, L. (2020). The neglected importance of floral traits in trait-based plant community assembly. Journal of Vegetation Science, 31(4), 529–539. https://doi.org/10.1111/jvs.12877

Endress, P. K. (2011). Evolutionary diversification of the flowers in angiosperms. American Journal of Botany, 98(3), 370–396. https://doi.org/10.3732/ajb.1000299

Endress, P. K. (2012). The Immense Diversity of Floral Monosymmetry and Asymmetry Across Angiosperms. Botanical Review, 78(4), 345–397. https://doi.org/10.1007/s12229-012-9106-3

Felsenstein, J. (1985). Phylogenies and the comparative method. American Naturalist, 125(1), 1–15. https://doi.org/10.1086/284325

Fenster, C. B., Armbruster, W. S., & Dudash, M. R. (2009). Specialization of flowers: Is floral orientation an overlooked first step?: Letters. New Phytologist, 183(3), 502–506. https://doi.org/10.1111/j.1469-8137.2009.02852.x

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution, and Systematics, 35, 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Fernández-Mazuecos, M., Blanco-Pastor, J. L., Gómez, J. M., & Vargas, P. (2013). Corolla morphology influences diversification rates in bifid toadflaxes (Linaria sect. Versicolores). Annals of Botany, 112(9), 1705–1722. https://doi.org/10.1093/aob/mct214

Fernández-Mazuecos, M., Blanco-Pastor, J. L., Juan, A., Carnicero, P., Forrest, A., Alarcón, M., Vargas, P., & Glover, B. J. (2019). Macroevolutionary dynamics of nectar spurs, a key evolutionary innovation. New Phytologist, 222(2), 1123–1138.

https://doi.org/10.1111/nph.15654

Freckleton, R. P. (2000). Phylogenetic tests of ecological and evolutionary hypotheses: Checking for phylogenetic independence. Functional Ecology, 14(1), 129–134. https://doi.org/10.1046/j.1365-2435.2000.00400.x

Garamszegi, L. Z. (2014). Modern phylogenetic comparative methods and their application in evolutionary biology. In Modern Phylogenetic Comparative Methods and their Application in Evolutionary Biology. https://doi.org/10.1007/978-3-662-43550-2

Gaston, K. J. (1994). Rarity. In Population and Community Biology Series.

Gaston, K. J. (2010). Valuing common species. Science, 327(5962), 154–155. https://doi.org/10.1126/science.1182818

Grant, V. (1984). Pollination Systems as Isolating Mechanisms in Angiosperms. Evolution, 3(1), 82–97. https://www-jstor-org.ezproxy.umsl.edu/stable/2405454?seq=1#metadata_info_tab_contents

Hamon, L. J. (2019). Phylogenetic comparative methods. https://doi.org/10.1016/j.cub.2017.03.049

Harmon, L. (2019). Phylogenetic comparative methods. https://doi.org/10.1016/j.cub.2017.03.049

Harper, K. T. (1979). Some Reproductive and Life History Characteristics of Rare Plants and Implications of Management. Great Basin Naturalist Memoirs, 3, 129–137. https://www.jstor.org/stable/23376606?seq=1#metadata_info_tab_contents

Harvey, P. H., & Pagel, M. D. (1991). The comparative method in evolutionary biology. Oxford: Oxford university press. http://www.sbs.utexas.edu/bio386/Readings/Text/Harvey.Ch.1.pdf

He, F., & Gaston, K. J. (2003). Occupancy, Spatial Variance, and the Abundance of

Species. American Naturalist, 162(3), 366–375. https://doi.org/10.1086/377190

Hernández-Hernández, T., & Wiens, J. J. (2020). Why Are There So Many Flowering Plants? A Multiscale Analysis of Plant Diversification. The American Naturalist, 195(6), 948–963. https://doi.org/10.1086/708273

Hileman, L. C. (2014). Trends in flower symmetry evolution revealed through phylogenetic and developmental genetic advances. Phil. Trans. R. Soc. B, 369. https://doi.org/10.1098/rstb.2013.0348

Ho, L. S. T., & Ané, C. (2014). Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. Methods in Ecology and Evolution, 5(11), 1133–1146. https://doi.org/10.1111/2041-210X.12285

Jin, Y., & Qian, H. (2019). V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography, 42(8), 1353–1359. https://doi.org/10.1111/ecog.04434

Joly, S., & Schoen, D. J. (2021). Repeated evolution of a reproductive polyphenism in plants is strongly associated with bilateral flower symmetry. Current Biology, 31(7), 1515-1520.e3. https://doi.org/10.1016/j.cub.2021.01.009

Kalisz, S., Ree, R. H., & Sargent, R. D. (2006). Linking floral symmetry genes to breeding system evolution. Trends in Plant Science, 11(12), 568–573. https://doi.org/10.1016/j.tplants.2006.10.005

Koch, C. U. von H. (2006). Secondary pollen presentation in Cuban bat pollinated Lobelia: precise deposition of pollen and mechanical species isolation. Botanische Jahrbücher Für Systematik, Pflanzengeschichte Und Pflanzengeographie, 127(1), 105–114. https://doi.org/10.1127/0006-8152/2006/0127-0105

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist, 149(4), 646–667. https://doi.org/10.1086/286013

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I., & White, E. P. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. In Ecology Letters (Vol. 10, Issue 10, pp. 995–1015). https://doi.org/10.1111/j.1461-0248.2007.01094.x

Moreira-Hernández, J. I., & Muchhala, N. (2019). Importance of Pollinator-Mediated Interspecific Pollen Transfer for Angiosperm Evolution. Annual Review of Ecology, Evolution, and Systematics, 50, 191–217. https://doi.org/10.1146/annurev-ecolsys-110218-024804

Muchhala, N. (2006). The pollination biology of Burmeistera (Campanulaceae): specialization and syndromes. American Journal of Botany, 93(8), 1081–1089. https://doi.org/10.3732/ajb.93.8.1081

Muchhala, N. (2007). Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. American Naturalist, 169(4), 494–504. https://doi.org/10.1086/512047

Neal, P. R., Dafni, A., & Giurfa, M. (1998). Floral symmetry and its role in plant-pollinator systems: Terminology, distribution, and hypotheses. Annual Review of Ecology and Systematics, 29, 345–373. https://doi.org/10.1146/annurev.ecolsys.29.1.345

O'Meara, B. C., Smith, S. D., Armbruster, W. S., Harder, L. D., Hardy, C. R., Hileman, L. C., Hufford, L., Litt, A., Magallón, S., Smith, S. A., Stevens, P. F., Fenster, C. B., & Diggle, P. K. (2016). Non-equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. Proceedings of the Royal Society B: Biological Sciences, 283(1830), 20152304. https://doi.org/10.1098/rspb.2015.2304

Ollerton, J., Alarcon, R., Waser, N. M., Price, M. V., Watts, S., Cranmer, L., Hingston, A., Peter, C. I., & Rotenberry, J. (2009). A global test of the pollination syndrome hypothesis. Annals of Botany, 103(9), 1471–1480. https://doi.org/10.1093/aob/mcp031

Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology, 48(3), 612–622. https://doi.org/10.1080/106351599260184

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics, 35(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2013). nlme: Linear and nonlinear mixed effects models. R Package Version 3(1),111, 128–185.

Rabinowitz, D. (1981). Seven forms of rarity. The Biological Aspects of Rare Plant Conservation, 205–217. https://doi.org/10.1177/004728702237415

Raiche, G., & Magis, D. (2020). Package "FSA" Title Simple Fisheries Stock Assessment Methods (pp. 1–58). https://github.com/droglenc/FSA

Revell, L. J. (2009). Size-correction and Principal components for Interspecific comparative studies. Evolution, 63(12), 3258–3268. https://doi.org/10.1111/j.1558-5646.2009.00804.x

Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution, 1(4), 319–329. https://doi.org/10.1111/j.2041-210x.2010.00044.x

Reyes, E., Sauquet, H., & Nadot, S. (2016). Perianth symmetry changed at least 199 times in angiosperm evolution. Taxon, 65(5), 945–964. https://doi.org/10.12705/655.1

Rudas Lleras, A., Prieto Cruz, A., Taylor, C. M. (Charlotte M., & Ortiz, R. (2005). Flórula del parque nacional natural amacayacu, amazonas, Colombia. https://agris.fao.org/agris-search/search.do?recordID=US201300105516

Sargent, R. D. (2004). Floral symmetry affects speciation rates in angiosperms. Proceedings of the Royal Society B: Biological Sciences, 271(1539), 603–608. https://doi.org/10.1098/rspb.2003.2644

Sauquet, H. (2021). Evolution: Cleistogamy to the rescue of zygomorphic flowers. Current Biology, 31(7), R332–R335. https://doi.org/10.1016/j.cub.2021.01.054

Sauquet, H., Carrive, L., Poullain, N., Sannier, J., Damerval, C., & Nadot, S. (2015). Zygomorphy evolved from disymmetry in Fumarioideae (Papaveraceae, Ranunculales): New evidence from an expanded molecular phylogenetic framework. Annals of Botany, 115(6), 895–914. https://doi.org/10.1093/aob/mcv020

Sauquet, H., Von Balthazar, M., Magallón, S., Doyle, J. A., Endress, P. K., Bailes, E. J., Barroso De Morais, E., Bull-Hereñu, K., Carrive, L., Chartier, M., Chomicki, G., Coiro, M., Cornette, R., El Ottra, J. H. L., Epicoco, C., Foster, C. S. P., Jabbour, F., Haevermans, A., Haevermans, T., … Schönenberger, J. (2017). The ancestral flower of angiosperms and its early diversification. Nature Communications, 8(1), 1–10. https://doi.org/10.1038/ncomms16047

Schluter, D. (2001). Ecology and the origin of species. In Trends in Ecology and Evolution (Vol. 16, Issue 7, pp. 372–380). Elsevier Current Trends. https://doi.org/10.1016/S0169-5347(01)02198-X

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. American Journal of Botany, 105(3), 302–314. https://doi.org/10.1002/ajb2.1019

Stebbins, G. L. (1970). Adaptive Radiation of Reproductive Characteristics in Angiosperms, I: Pollination Mechanisms. Annual Review of Ecology and Systematics, 1(1), 307–326. https://doi.org/10.1146/annurev.es.01.110170.001515

Steyermark, J. A., Berry, P. E., & Holst, B. K. (1995). Flora of the Venezuelan Guayana. In Missouri Botanical Garden (Vol. 1). https://doi.org/10.2307/1222619

Veeresh Kumar, Belavadi, V. V., Revanasidda, Tharini, K. B., & Srinivasa, Y. B. (2019). Stamen elongation in sunn hemp appears to allow delayed self-pollination in the absence of pollinators – A case of bet-hedging? South African Journal of Botany, 127, 110–116. https://doi.org/10.1016/j.sajb.2019.08.052

Vermeij, G. J., & Grosberg, R. K. (2018). Rarity and persistence. Ecology Letters, 21(1), 3–8. https://doi.org/10.1111/ele.12872

Wong Sato, A. A., & Kato, M. (2018). Breeding system and bumblebee drone pollination of an explosively pollen-releasing plant, Meliosma tenuis (Sabiaceae). Plant Biology, 20(3), 537–545. https://doi.org/10.1111/plb.12699

Yoder, J. B., Gomez, G., & Carlson, C. J. (2020). Zygomorphic flowers have fewer potential pollinator species. Biology Letters, 16(9), 20200307. https://doi.org/10.1098/rsbl.2020.0307

Zhao, Z. G., & Wang, Y. K. (2015). Selection by pollinators on floral traits in generalized Trollius ranunculoides (Ranunculaceae) along altitudinal gradients. PLoS ONE, 10(2). https://doi.org/10.1371/journal.pone.0118299

FIGURES AND TABLES

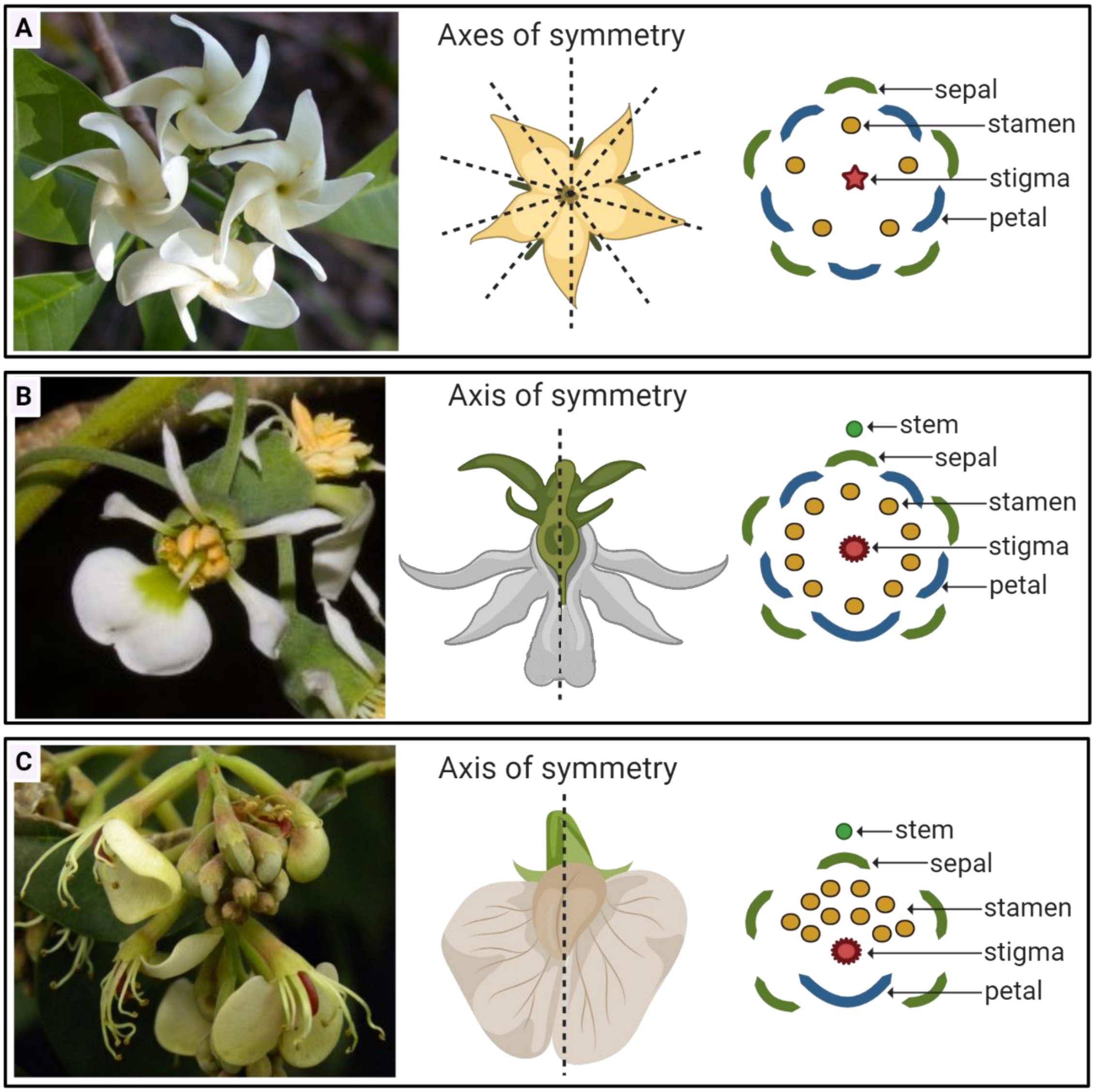

Figure 1. Depiction of the two major types of floral symmetry: A) actinomorphic corolla, B) zygomorphic corolla and actinomorphic gynoecium and androecium, and C) zygomorphic corolla and zygomorphic androecium. The species are found in the Madidi forest database, and the photos are from Tropicos. The species A) Tabernaemontana cymose, B) Myroxylon peruiferum and C) Amburana cearensis. Based on Kalisz et al., (2006) and Sauquet et al., (2015).

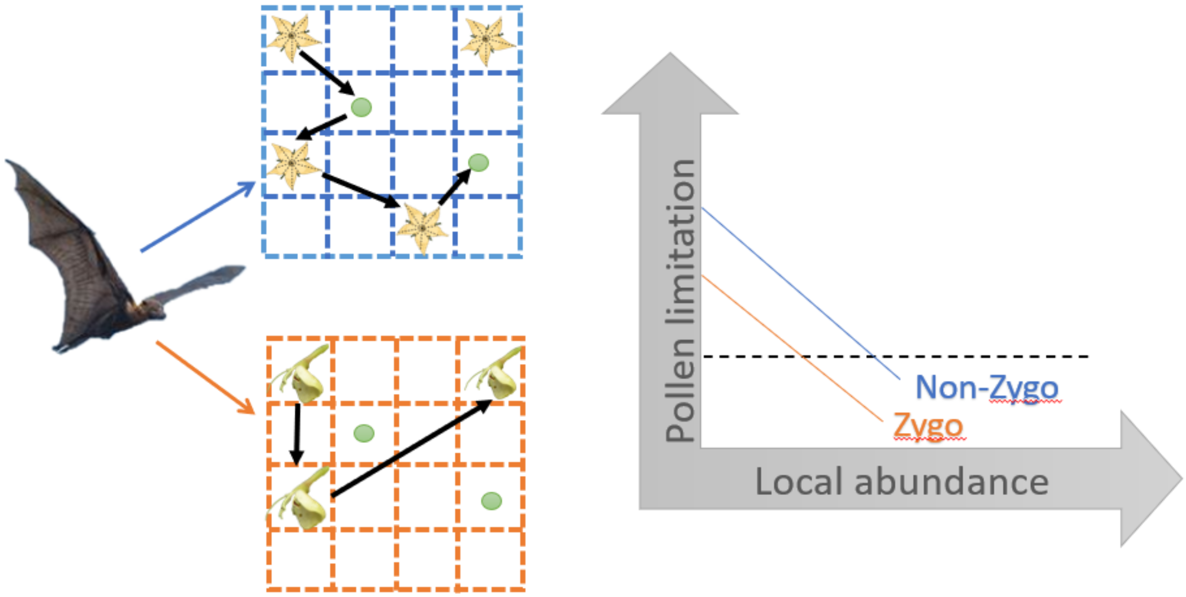

Figure 2. Representation of the pollination of a population with specialized zygomorphic flowers vs. non-specialized actinomorphic flowers. The bat pollinator approaches the actinomorphic flowers sporadically, collects and transmits pollen between flowers from different species. Whereas the foraging trip of the bat is more effective because it approaches only the specialized zygomorphic flowers and transmits the pollen between conspecific flowers. This behavior has a differential effect in the number of individuals that contribute to an effective reproduction and at what critical threshold (dashed black line) there is pollen limitation.

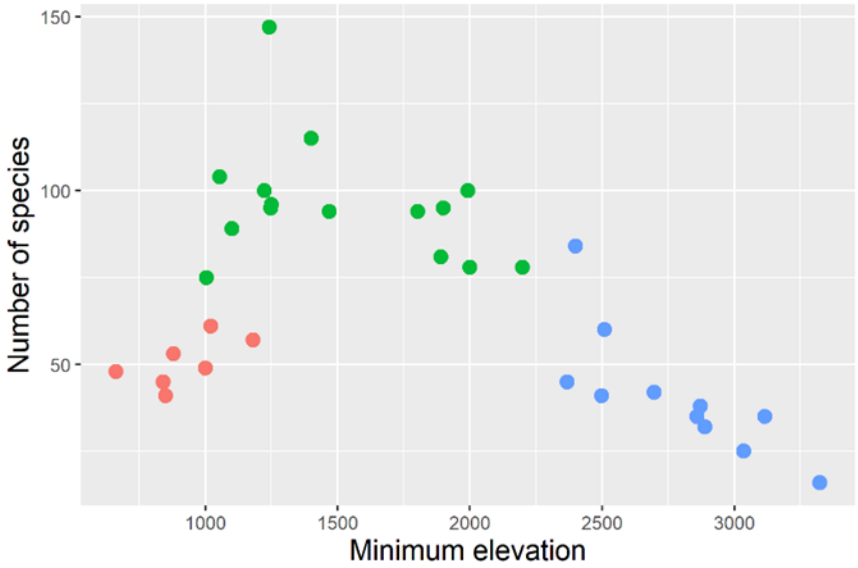

Figure 3. Diversity and elevation by forest type. Each data point depicts a 1ha plot, showing their number of species and elevation. The red plots belong to (a) dry forest, the green to (b) sub-humid and humid forest, and the blue to (c) upper montane forest. Forest types differ dramatically in species composition, as well as in environmental conditions along the elevational gradient.

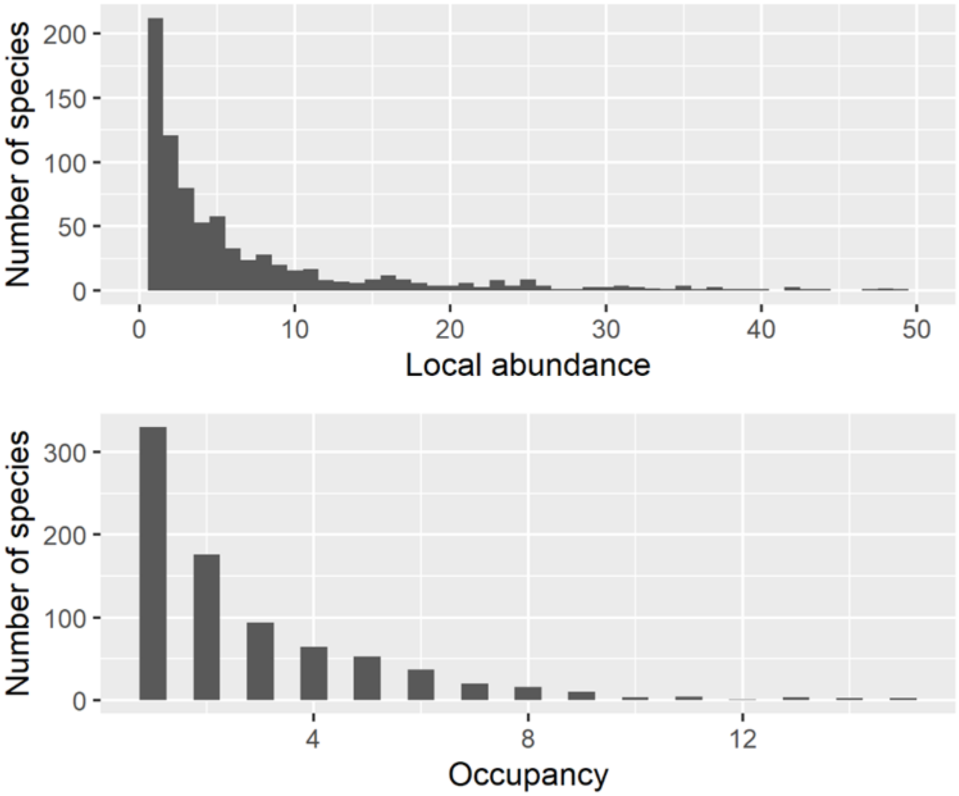

Figure 4. Distribution of the local abundance and occupancy of species. For better visualization of the species frequencies, 16 species that present higher local abundance than 50 individuals are excluded from the top panel.

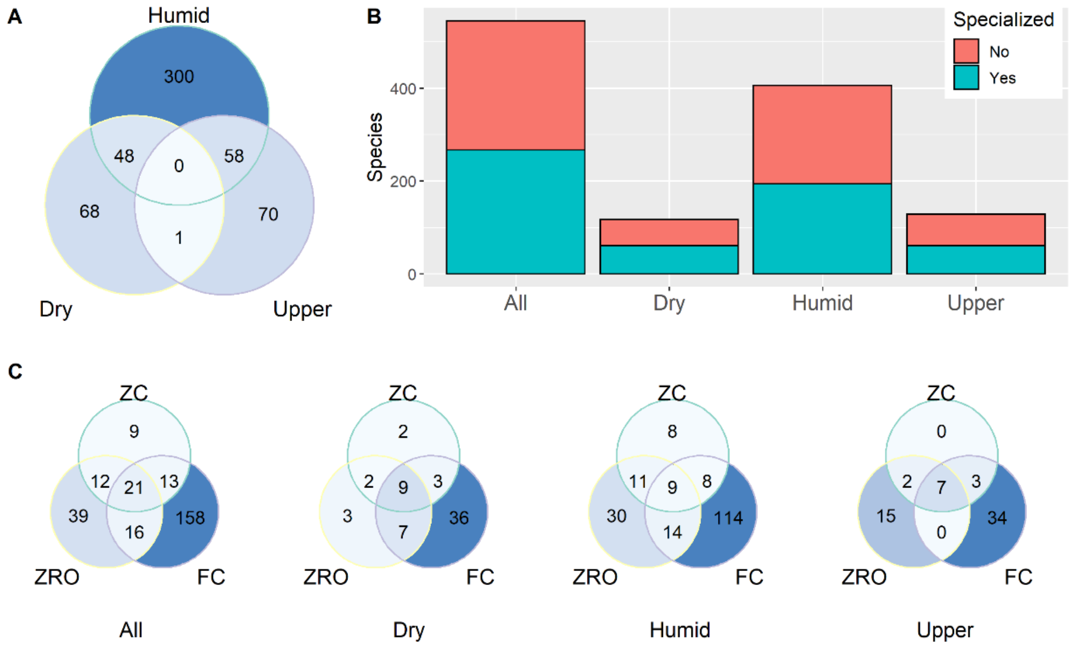

Figure 5. Distribution of the species floral traits overall and for each forest type. A) Partition of the total 545 species in the dry, sub-humid and humid, and upper montane forests. Some species are shared between two forests but none by three forests; B) Number of species with floral specialization; C) Decomposition of the specialized species that presented at least one floral trait, zygomorphic corolla (ZC), zygomorphic reproductive organs (ZRO), and/or fused or tubular corolla (FC).

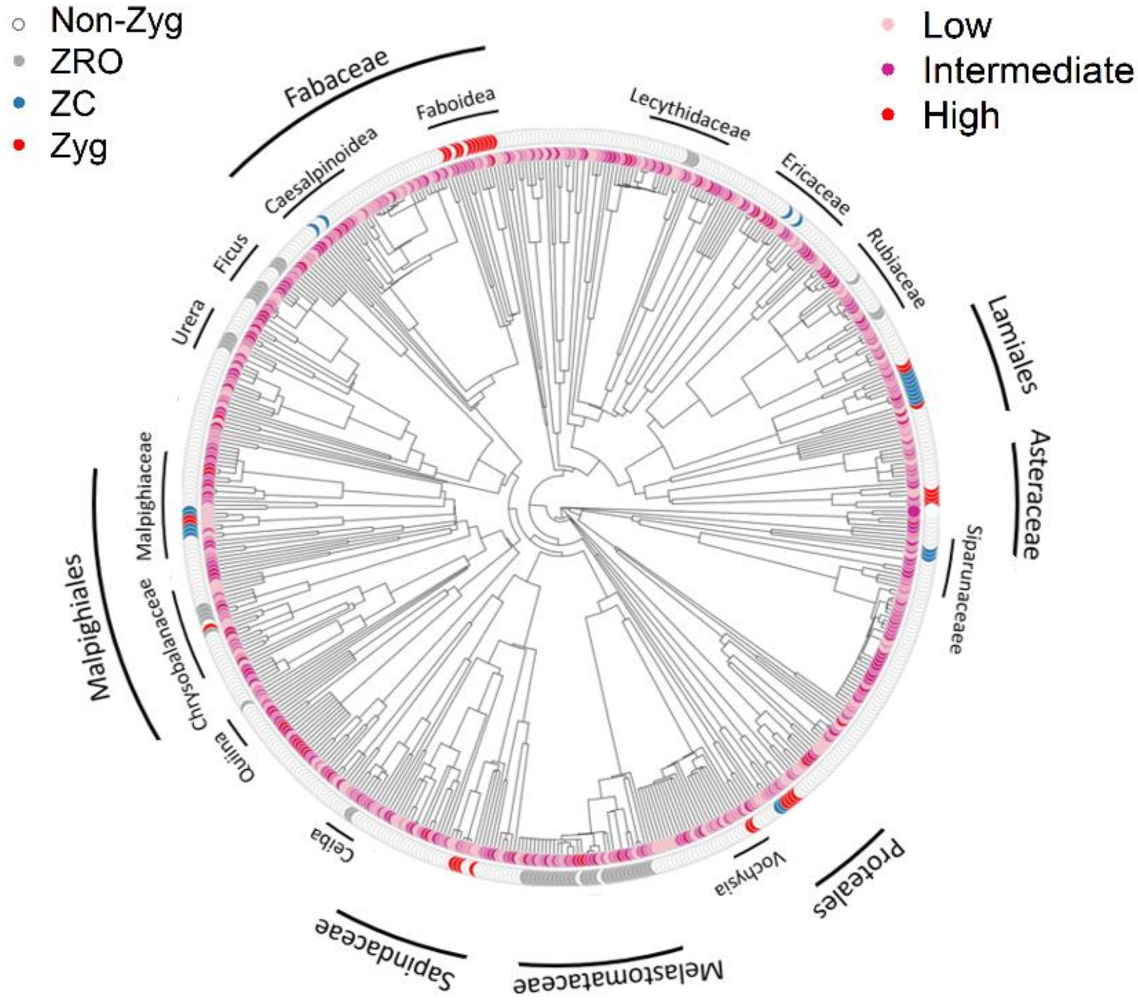

Figure 6. Phylogeny of the 545 tree species. The first ring around the tips represents the gradient of species abundance from low (pink) to high (red). The second ring represents zygomorphy in the reproductive organs (ZRO in gray), corolla (ZC in blue) and both (Zyg in red).

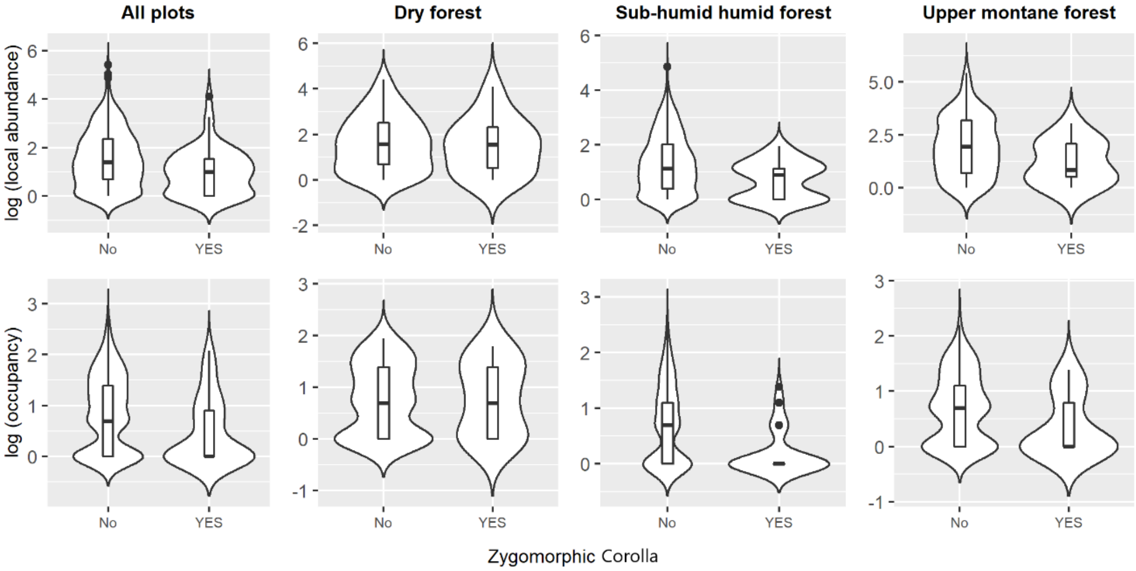

Figure 7. Abundance of species between species with zygomorphic (YES) and non-zygomorphic corolla.

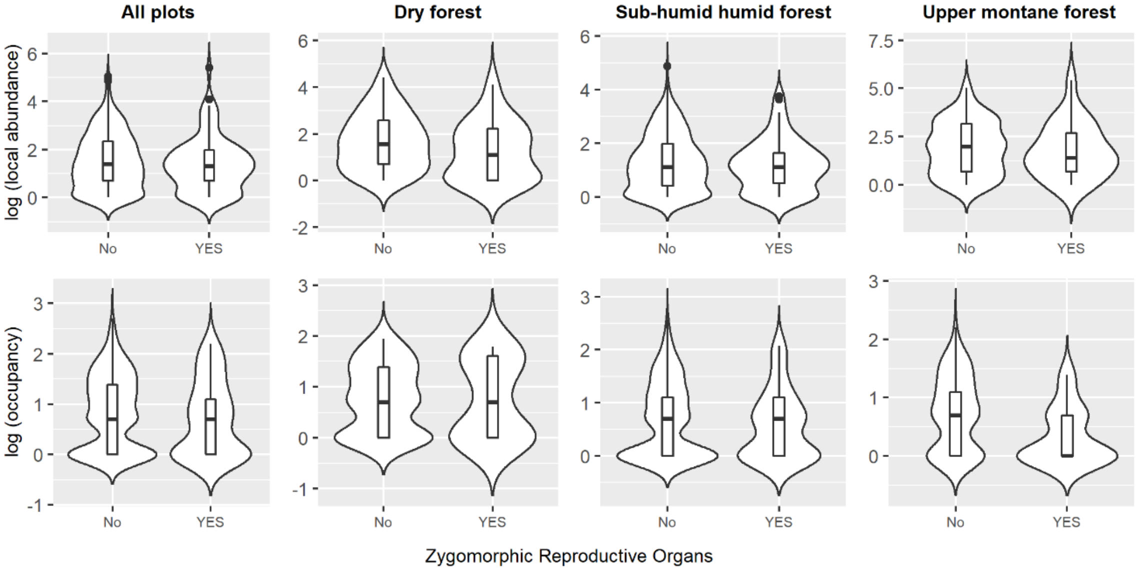

Figure 8. Abundance of species between species with zygomorphic (YES) and non-zygomorphic reproductive organs.

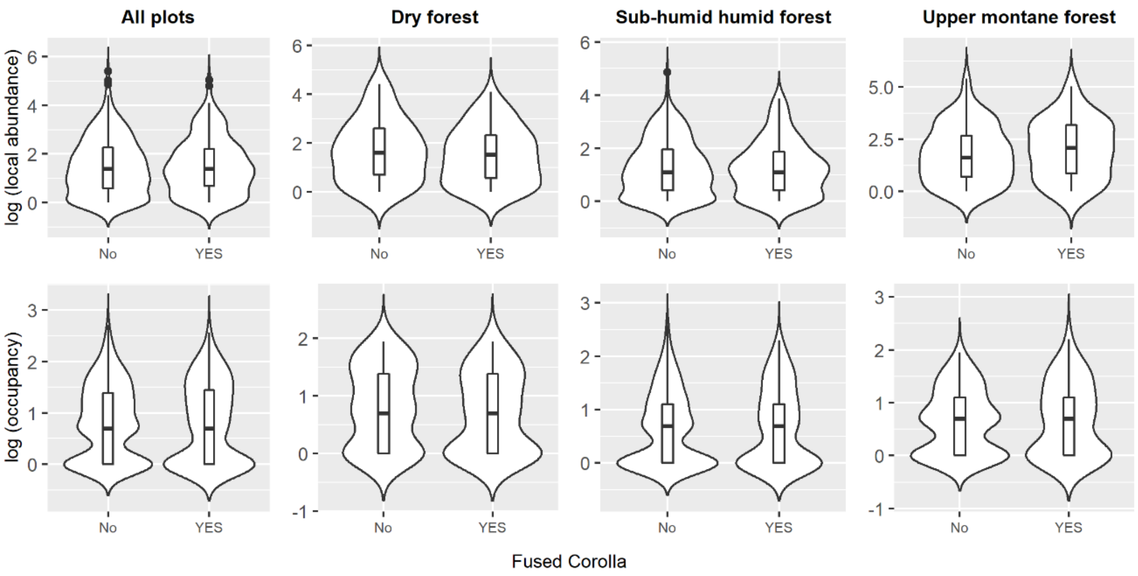

Figure 9. Abundance of species between species with fused/tubular (YES) and free petals.

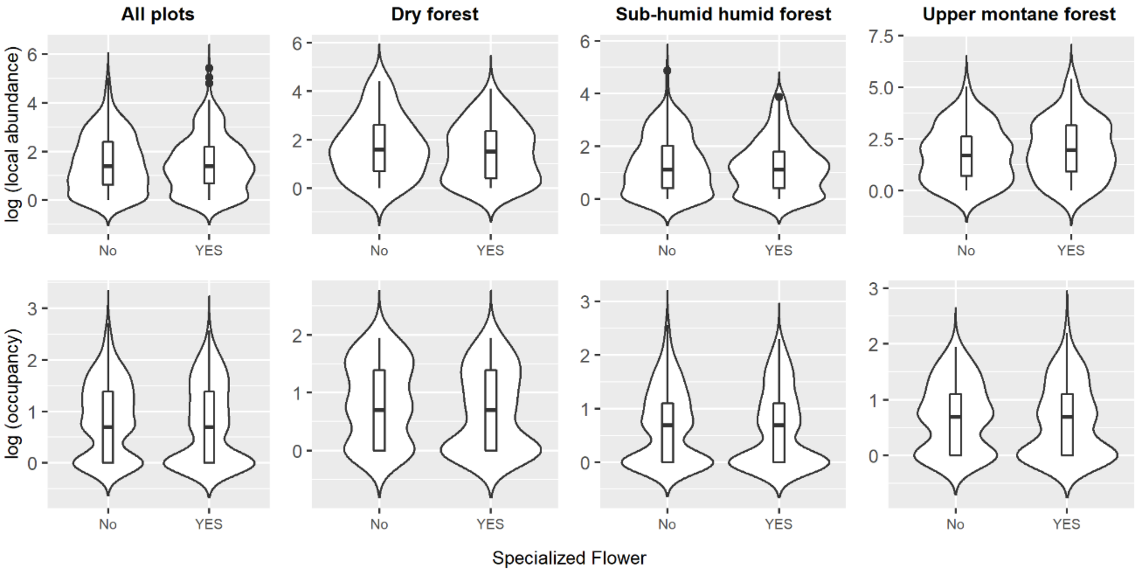

Figure 10. Abundance of species between species with specialized (YES) and non-specialized flower.

Table 1. Parameter estimates of the abundance regression between species with zygomorphic and non-zygomorphic corolla. The parameters B0: intercept, B1: slope, p-value, AIC: Akaike information criterion, R2, λ: phylogenetic signal, p-BH: Benjamini and Hochberg (BH) false discovery rate correction are reported for ordinary least squares (OLS) and Pagel's λ phylogenetic correction regression (PGLS).

		OLS			**PGLS**						
		p	**AIC**	**R2**	**B0**	**B1**	**p**	**AIC**	**R2**	**λ**	**p-BH**
Abundance	**All**	9.47E-04	1701.5	1.99E-02	1.53	-0.52	6.29E-03	1693.6	1.37E-02	0.142	0.05
	Dry	0.691	383	1.38E-03	1.82	-0.19	0.567	384.8	2.85E-03	0.050	-
	Humid	1.12E-03	1178.3	2.60E-02	1.30	-0.51	1.18E-02	1174.7	1.56E-02	0.121	-
	Upper	0.071	447.6	2.55E-02	2.48	-0.63	0.170	445.1	1.48E-02	0.177	-
Occupancy	**All**	1.99E-04	1211	2.52E-02	1.25	-0.39	2.54E-04	1213	2.44E-02	0.007	0.04
	Dry	0.891	248.6	1.65E-04	0.73	0.03	0.891	250.5	1.65E-04	1.00E-07	-
	Humid	2.71E-05	841.2	4.27E-02	0.69	-0.50	2.71E-05	843.2	4.27E-02	1.00E-07	-
	Upper	0.085	245.6	2.32E-02	1.00	-0.30	0.134	245	1.76E-02	0.107	-

Table 2. Parameter estimates of the abundance regression between species with zygomorphic and non-zygomorphic reproductive organs. The parameters B0: intercept, B1: slope, p-value, AIC: Akaike information criterion, R2, ʎ: phylogenetic signal, p-BH: Benjamini and Hochberg (BH) false discovery rate correction are reported for ordinary least squares (OLS) and Pagel's ʎ phylogenetic correction regression (PGLS).

		OLS			**PGLS**						
		p	**AIC**	**R2**	**B0**	**B1**	**p**	**AIC**	**R2**	**ʎ**	**p-BH**
Abundance	**All**	0.397	1711.80	1.32E-03	1.72	-0.24	0.136	1698.64	4.09E-03	0.170	0.46
	Dry	0.151	381.05	1.78E-02	2.15	-0.47	0.122	382.67	2.07E-02	0.056	-
	Humid	0.480	1188.53	1.24E-03	1.51	-0.24	0.145	1178.38	5.24E-03	0.189	-
	Upper	0.659	450.70	1.54E-03	1.88	-0.09	0.810	446.90	4.55E-04	0.198	-
Occupancy	**All**	0.129	1222.61	4.23E-03	0.95	-0.12	0.199	1224.20	3.04E-03	0.020	0.49
	Dry	0.855	248.54	2.90E-04	0.80	-0.03	0.855	250.54	2.90E-04	1.00E-07	-
	Humid	0.298	857.82	2.68E-03	0.76	-0.10	0.307	858.73	2.58E-03	0.039	-
	Upper	5.25E-03	240.65	5.97E-02	1.11	-0.39	5.25E-03	242.65	5.97E-02	1.00E-07	-

Table 3. Parameter estimates of the abundance regression between species with tubular/fused and free corolla. The parameters B0: intercept, B1: slope, p-value, AIC: Akaike information criterion, R2, ƛ: phylogenetic signal, p-BH: Benjamini and Hochberg (BH) false discovery rate correction are reported for ordinary least squares (OLS) and Pagel's ƛ phylogenetic correction regression (PGLS).

		OLS			**PGLS**						
		p	**AIC**	**R^2**	**B_0**	**B_1**	**p**	**AIC**	**R^2**	**ƛ**	**p-BH**
Abundance	**All**	9.10E-01	1712.51	2.37E-05	1.38904	0.05283	7.00E-01	1700.73	2.74E-04	0.16758	0.87
	Dry	0.35281	382.274	7.51E-03	1.94712	-0.2376	0.31655	384.058	8.72E-03	0.04344	-
	Humid	9.03E-01	1189.02	3.68E-05	1.28293	-0.0375	7.93E-01	1180.42	1.70E-04	0.17972	-
	Upper	0.3713	450.087	6.30E-03	1.35101	0.32148	0.30462	445.879	8.30E-03	0.20347	-
Occupancy	**All**	6.77E-01	1224.75	3.21E-04	0.8517	-0.0247	7.37E-01	1225.63	2.08E-04	0.03094	0.87
	Dry	0.40276	247.862	6.10E-03	0.918	-0.1067	0.40276	249.862	6.10E-03	1.00E-07	-
	Humid	5.59E-01	858.566	8.46E-04	0.58489	0.04658	5.64E-01	859.443	8.24E-04	3.55E-02	-
	Upper	0.76768	248.503	6.90E-04	0.64365	0.0217	0.87329	247.153	2.01E-04	0.13203	-

Table 4. Parameter estimates of the abundance regression between species with specialized and non-specialized flower. The parameters B0: intercept, B1: slope, p-value, AIC: Akaike information criterion, R2, ʎ: phylogenetic signal, p-BH: Benjamini and Hochberg (BH) false discovery rate correction are reported for ordinary least squares (OLS) and Pagel's ʎ phylogenetic correction regression (PGLS).

		OLS			**PGLS**						
		p	**AIC**	**R^2**	**B_0**	**B_1**	**p**	**AIC**	**R^2**	**ʎ**	**p-BH**
Abundance	**All**	6.70E-01	1712.34	3.34E-04	1.54242	-0.0625	6.20E-01	1700.63	4.52E-04	0.16736	0.83
	Dry	0.2706	381.916	1.05E-02	2.01158	-0.2723	0.24625	383.706	1.17E-02	0.04182	-
	Humid	4.35E-01	1188.42	1.51E-03	1.42936	-0.1402	2.87E-01	1179.35	2.81E-03	0.18256	-
	Upper	0.32624	449.919	7.59E-03	1.34895	0.29985	0.29104	445.82	8.77E-03	0.20916	-
Occupancy	**All**	5.30E-02	1221.17	6.88E-03	0.98825	-0.1167	8.25E-02	1222.9	5.54E-03	0.01647	0.44
	Dry	0.19735	246.879	1.44E-02	1.01053	-0.164	0.19735	248.879	1.44E-02	1.00E-07	-
	Humid	4.62E-01	858.365	1.34E-03	0.72124	-0.0532	4.86E-01	859.287	1.20E-03	3.93E-02	-
	Upper	0.3745	247.788	6.22E-03	0.73244	-0.043	0.72811	247.062	9.55E-04	0.12417	-