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TITLE: The level of pollination specialization affects the relationship between the shape of flowers and the bill of their hummingbird pollinators in Antillean Gesneriaceae

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Running head: Flower and bill shape covariation in Gesneriaceae

ABSTRACT

- *Premise of the Research*: Pollinators are known to impose strong selection on floral shape. Particularly well studied is the relationship between the flowers of hummingbird-pollinated plant species and the bills of their pollinators. However, no studies to date have evaluated whether these relationships vary according to the level of pollination specialization. Here we quantify the relationship between the corolla shape of Antillean Gesneriaceae and the bill of their hummingbird pollinators for species with a specialist (one functional group of pollinators: hummingbirds) and a generalist pollination strategy (more than one functional group of pollinators: hummingbirds, bats, and insects).

- *Methodology*: We used phylogenetic generalized least squares analyses on linear measurements and phylogenetic two blocks partial least squares on multivariate geometric morphometrics data to test if and how the variation in corolla shape of the Antillean Gesneriaceae is correlated to the shape of the bill of their hummingbird pollinators.

- *Pivotal Results*: We found that corolla shape is correlated with the bill shape of their hummingbird pollinators, but that the nature of this relationship differed between pollination specialists and generalists. For example, curved corollas were positively correlated with curved bills for specialists, but not for generalists.

- *Conclusions*: Our study suggests that pollinators affect the evolution of flower shape but that the nature and strength of the selective pressures are affected by the pollinator guild of the pollinators in the Antillean Gesneriaceae.

INTRODUCTION

Flowering plants experience persistent selection on reproductive traits to ensure sexual reproduction (Cresswell, 1998). For animal-pollinated species, selection on floral traits is often mediated by pollinators in traits related to pollinator attraction, pollen removal, and pollen deposition (Armbruster *et al.*, 2014). Such selection pressures imposed by specific pollinators often lead to the evolution of similar traits in independent evolutionary lineages—i.e., the concept of pollination syndromes (Faegri & Van Der Pijl, 1979). Many such convergent floral traits are well known (Fenster *et al.*, 2004; Rosas-Guerrero *et al.*, 2014), such as red tubular flowers for hummingbird-pollinated plants, or bell-shaped, light-colored, nocturnal flowers for bat-pollinated plants (Baker, 1961).

The relationship between hummingbirds and hummingbird-pollinated plants has long fascinated botanists and evolutionary biologists (Darwin, 1876) and the hummingbird pollination syndrome is one of best supported patterns of floral convergence (Rosas-Guerrero *et al.*, 2014). Plant-hummingbird interactions are often asymmetric, and most hummingbirds are generalist pollinators that visit several plant species (Abrahamczyk *et al.*, 2015; Dalsgaard *et al.*, 2008; del Coro Arizmendi & Ornelas, 1990; Ollerton *et al.*, 2007; Snow & Snow, 1980). Moreover, while hummingbirds commonly visit plants species with ornithophilous flowers, they can also visit plants that are primarily pollinated by insects or bats (Abrahamczyk & Kessler, 2010; Abrahamczyk & Kessler, 2015; Araujo & Sazima, 2003). Conversely, flowers that fit the hummingbird pollination syndrome may also be pollinated by other types of floral visitors (Castellanos *et al.*, 2003; Etcheverry *et al.*, 2012; Muchhala & Thomson, 2010) or possess adaptations to deter other types of pollinators, such as the narrow corolla of some hummingbird-pollinated species (Clark *et al.*,

2015; Castellanos *et al.*, 2004; Pellmyr, 2002). Interestingly, both theoretical and empirical studies have shown that even minor pollinators can affect the evolution of floral traits (Aigner, 2001; Aigner, 2006; Mayfield *et al.*, 2001). As such, hummingbirds have the potential to influence the floral shape of the plant species they pollinate, even for species for which they are a minor contributor to the pollination success.

The association between floral shape and the mouthparts of their pollinators has been the focus of several studies (Agosta & Janzen, 2005; Dalsgaard *et al.*, 2009; Sonne *et al.*, 2020; Temeles & Kress, 2003; Van der Niet *et al.*, 2014). This association is expected to be important for the mechanical fit, proper pollen export, and pollen deposition. Several studies have shown a strong positive correlation between hummingbird bill length and corolla tube length of the flower they pollinate (Cotton, 1998; Dalsgaard *et al.*, 2009; del Coro Arizmendi & Ornelas, 1990; Maglianesi *et al.*, 2014; Nattero & Cocucci, 2007); however, the relationship is generally not perfect (Cotton, 1998; Maglianesi *et al.*, 2014). As mentioned above, hummingbirds are usually generalists and they often use plants with a broad range of corolla lengths (Araujo & Sazima, 2003; del Coro Arizmendi & Ornelas, 1990). In fact, controlled experiments have shown that hummingbirds tend to prefer feeding on short and straight (i.e., non-curved) corollas (Maglianesi *et al.*, 2015; Temeles *et al.*, 2009). The contrast between such findings obtained in controlled environments and the observed correlations between corolla length and bill length observed in nature (see Maglianesi *et al.*, 2015 for a comparison of experimental and natural conditions) could be explained by niche partitioning, where competition for limited resources could lead to plant-pollinator co-adaptation (Kodric-Brown *et al.*, 1984; Maglianesi *et al.*, 2015; Temeles *et al.*, 2013). In addition, there is evidence of a correlation between corolla length and nectar volume (del Coro Arizmendi &

Ornelas, 1990; Kodric-Brown *et al.*, 1984), and of reduced handling times by hummingbirds in flowers that better fit their bills (Maglianesi *et al.*, 2014).

Beyond strict length comparisons, the fit between the shape of hummingbird bills and the corollas they pollinate has also attracted much interest (Stiles, 1975; Temeles *et al.*, 2000), although few studies have quantified this relationship in natural communities or within a comparative framework. One exception is the study by Maglianesi et al. (2014) that found significant correlations between bill curvature and corolla curvature, as well as between hummingbird body mass and the volume of corollas in three ecological communities of Costa Rica. Several methods are now available to study the overall shape of organisms, such as geometric morphometrics or elliptical Fourrier analysis, and they have been used recently to study bird bill shape evolution (Berns & Adams, 2010; Foster *et al.*, 2008; Navalón *et al.* 2019) and corolla shape evolution (e.g., Gómez *et al.*, 2016; Joly *et al.*, 2018; Smith & Kriebel, 2018; Strelin et al. 2019). However, these methods have yet to be used to correlate flower and bill shapes.

The subtribe Gesneriinae (Gesneriaceae) is a great clade for investigating the relationship between the floral shape and the bill shape of their hummingbird pollinators because it represents a monophyletic lineage of 94 species that diversified in the Caribbean and it exhibits a broad range of corolla shapes (Martén-Rodríguez *et al.*, 2010). Pollinator information in the group is supported by high-quality pollination data (Faure & Joly, 2020; Martén-Rodríguez & Fenster, 2008; Martén-Rodríguez *et al.*, 2009; Martén-Rodríguez *et al.*, 2010; Martén-Rodríguez *et al.*, 2015). Most species are visited by hummingbirds (Martén-Rodríguez *et al.*, 2009; Martén-Rodríguez *et al.*, 2015), but these species fall into two main pollination strategies. Some are specialists, pollinated exclusively or almost exclusively (>80%) by hummingbirds, while others have a mixed pollination

strategy and are also pollinated by other functional types of pollinators (e.g., perching birds, bats, flies, or moths). In these functional generalist species, hummingbirds represent 20% to 65% of all pollinator visits (Martén-Rodríguez *et al.*, 2015). The presence of these syndromes and their repeated evolution (Martén-Rodríguez *et al.*, 2010; Joly et al., 2018) allows us to quantify and compare the degree of fit between the bill shape of hummingbirds and the corolla shape of species with specialist and generalist strategies. One interesting aspect of this plant group is the variation observed in floral shapes within syndromes, which parallels the variation observed in the length and curvature of the bills of hummingbirds observed across the Greater Antilles (Figure 1). Moreover, floral length and curvature (Joly *et al.*, 2018) have been demonstrated to be under strong genetic control (Alexandre *et al.*, 2015). In the most recent taxonomic treatment of *Gesneria*, Skog (1976) also suggested a correlation between the sizes and shapes of flowers and their putative hummingbird and bat pollinators, but the absence of pollinator data at that time did not allow him to formally test these hypotheses.

In this study, we used univariate measurements and geometric morphometric approaches to test if the variation in the floral shape of Gesneriaceae species can be explained by the variation in the bill shape of their hummingbird pollinators and if these relationships were affected by the degree of pollination specialization of the plant species. Given the variable and reduced importance of hummingbirds in the reproductive success of pollination generalists in contrast with specialists, we expect the correlation between corolla and bill shapes to be of lesser importance for the generalist pollination strategy.

METHODS

The Antillean Gesneriaceae

The subtribe Gesneriinae (Gesneriaceae) consists of 94 species: 65 species of *Gesneria*, 25 of *Rhytidophyllum,* two species of *Pheidonocarpa,* and two species of *Bellonia* (Clark *et al.*, 2020). All except five species occur in the Greater Antilles (Cuba, Jamaica, Puerto Rico, and Hispaniola). Two species are found in the Lesser Antilles and two in northern South America. Most species can be classified into three main pollination syndromes: hummingbird pollination, bat pollination, and a mixed-pollination syndrome in which species are pollinated by hummingbirds, bats and insects (Martén-Rodríguez *et al.*, 2009). The species pollinated by hummingbirds have tubular flowers, often red or yellow (Figure 1 A, B), the species pollinated by bats have bell-shaped, green or white flowers, and the mixed-pollination species, henceforth also called generalists, have subcampanulate flowers with a constriction at the base that may be of various colors, including spotted patterns (Figure 1 C). Here, we studied 18 species pollinated by hummingbirds, nine specialists, and nine generalists, for which we had morphometric data and pollination information from field observations (Table 1).

Hummingbirds of the Greater Antilles

At least forty species of hummingbirds (Trochilidae) can be found in the Caribbean but we only considered the hummingbird species occurring in the Greater Antilles (Table 2, information from GBIF.org, accessed in May 2020) as no plant species from the Lesser Antilles were included in our study. Pollinator information was obtained from previous field studies (Martén-Rodríguez & Fenster, 2008; Martén-Rodríguez *et al.*, 2009; Martén-Rodríguez *et al.*, 2010; Martén-Rodríguez *et al.*, 2015). These studies showed that only seven species of hummingbirds were observed

pollinating Gesneriaceae species and that in general only one or two hummingbird species pollinate any single plant species (Tables 1 and 2).

Corolla shape

For each plant species, corolla shape was quantified using the raw geometric morphometric data from Joly et al. (2018). We had photographs for 71 flowers at anthesis in longitudinal view for the 18 species studied. Each flower was characterized by six landmarks (two at the base of the corolla, two at the tips of the petal lobes, and two at the base of the corolla tube opening) and 13 semi-landmarks positioned at equal distance following the curve on each side of the corolla (Figure 2 A). Each flower was landmarked twice to quantify the error associated with the positioning of landmarks.

The raw landmark data was transformed by generalized Procrustes analysis in R (R core team 2014) with the geomorph R package (Adams *et al.*, 2016). The semi-landmarks were superimposed by minimizing the Procrustes distance between the reference and the target species. To represent the floral morphospace, a principal component analysis (PCA) of the covariance matrix was performed using the 'prcomp' function in R, and mean shapes per species were calculated from the intraspecific samples.

We considered floral length and curvature as univariate characters. Flower length was measured as the distance between the base of the corolla and the aperture of the adaxial side of the corolla (further referred to as top corolla length). This measurement of flower length seems more relevant

in a pollination context as it correlates more closely with the placement of the reproductive organs in this group (anthers and stigma), but we also considered the length of the abaxial side of the corolla in our analyses (bottom corolla length). Corolla lengths were measured from photographs in longitudinal view obtained from herbarium specimens (NY) or taken in the field from exploratory research expeditions done by Clark, as well as from specimens of the Montreal Botanical Garden collections (Supplementary Table A1). Flower curvature was estimated from the landmarks using the angle formed between a line connecting the two landmarks at the base of the flower and another line that passes through the two landmarks at the corolla opening (Alexandre *et al.*, 2015); a greater angle indicates greater curvature (Figure 2 C).

Hummingbird bill shape

The bill shape of hummingbirds was quantified from pictures of all hummingbird species occurring on the four largest Antillean islands (e.g., Cuba, Jamaica, Puerto Rico, and Hispaniola). The images of the hummingbird bills in longitudinal view were obtained from several websites with the authorization of the photographers, and additional photographs were provided directly by photographers (Supplementary Table A2). We only retained images for which the bill of the bird was in profile view and the photograph taken perpendicularly to the bill. In total, 103 images were studied for 14 species and each species was represented by at least six images (Table 2). The sex of the hummingbirds was recorded for species that have a clear dimorphism. Not all species of Antillean hummingbirds studied are observed pollinators of gesneriads, but all species present in the Greater Antilles were included in the morphometric analysis to contrast the bill shapes of those species that actually visit and carry pollen from Gesneriinae flowers (pollinators) and those were never observed visiting the study species.

The bill shape was quantified using a geometric morphometrics approach similar to the one used for the flowers and to previous studies of bill shape (Berns & Adams, 2010; Foster *et al.*, 2008). Each image was duplicated and the landmarks were positioned on each duplicate to quantify the error involved in landmark positioning. For each picture, three landmarks and 20 semi-landmarks were positioned with the software TpsDig (Rohlf, 2004). Two landmarks were placed at the base of the bill (i.e., base of the top mandible and base of the bottom mandible) and one at the tip. Ten equidistant semi-landmarks were then placed along the curve of the upper and bottom part of the bill, between the base and tip landmarks (Figure 2 B). A Procrustes analysis was done to superimpose the different bill shapes. A PCA was done on the bill's landmark measurements of all the hummingbird species to illustrate the variation in bill shape among the species.

Bill curvature was measured using a similar approach to the one used for corolla curvature. We measured the angle formed between lines passing through the two landmarks at the base of the bill and the two semi-landmarks adjacent to the landmark at the tip of the bill (Figure 2 D).

For both flowers and bills, a scale was not available for all pictures, so we could not remove the effect of size in the morphometric data using regression. However, the effect of size was removed in the Procrustes analysis by scaling all specimens to the same centroid size.

Statistical analyses

A Procrustes ANOVA was performed on the corolla shape data to partition the variability in corolla shape between species. Similarly, a Procrustes ANOVA was performed on bill shape data to test if

the bill shape of hummingbirds differs according to different factors: gender, species, and if the species is a known pollinator or not. Procrustes ANOVA was also used to quantify the error involved in the positioning of the landmarks. The ANOVAs were performed using the function 'procD.lm' of the package "geormorph" (Adams et al. 2016) in R (R core team, 2020).

To test the hypothesis that floral shape could be explained by variation in hummingbird bill shape, we considered the following three components of flower and bill shapes: length, curvature and global shape as determined by the geometric morphometric. Only hummingbird species that are known to pollinate gesneriads were included in bill – flower comparisons. The correlation between the flower and bill morphologies was tested using two approaches: one analysis for univariate measurements and one analysis for morphometric data. In both cases, the flowers pollinated by more than one hummingbird species were duplicated in the dataset to have each combination represented. The species means were used in the analyses of the flowers and bill measurements and shapes.

First, the effect of length and curvature of the hummingbird bill on flower length and curvature was tested using phylogenetic generalized least squares (PGLS) using the plant phylogeny of Joly et al. (2018). The PGLS model was fitted using the 'gls' function of the nlme R package (Pinheiro et al., 2020) and the Pagel (1999) phylogenetic correlation structure from the ape R package (Paradis and Schliep, 2019). The use of the Pagel correlation structure allows the residuals of the model to be adjusted according to the adequate level of phylogenetic correlation, which is important for the analysis to be unbiased (Revell, 2010). We tested the length or curvature of the bill with the pollination syndrome (specialist or generalist) and the interaction term. The lambda parameter of the Pagel correlation structure was first obtained with the full model using restricted

maximum likelihood (REML). The fixed effects were then tested using the 'anova' function between the models fitted by maximum likelihood (ML) with the lambda parameters treated as fixed. The best model was finally refitted using REML, optimizing the lambda parameter, to get the parameters of the model. Normality of normalized residuals was verified for all analyses.

Second, we compared directly the full shapes of flowers with those of the bill of their pollinators using a phylogenetic two blocks partial least square analysis (2B-PLS: Rohlf et al. 2002; Adams and Felice, 2014) using the same plant phylogeny as above. This was performed separately for the specialists and the generalist because the analysis could not account for an interaction term and because some of the PGLS found the interaction term to be significant (see below). The phylogenetic 2B-PLS was performed using the 'phylo.integration' function of the geomorph R Package. The data and script to perform the analyses are provided as supplementary material.

RESULTS

Variation of the corolla shape

The corolla morphospace illustrates variation in corolla shape among the studied species and broadly differentiates hummingbird specialist flowers from generalist flowers (Figure 3). The first principal component (PC) represents 65.8% of the total shape variance and shows variation from tubular shapes typical of hummingbird specialists to the right to subcampanulate (bell-shaped with basal constriction) corolla shapes that are characteristic of generalist flowers to the left. The second PC explains 12.5% of the variance and is characterized by the corolla curvature. The third component explains 9.0% of the variation and represents the extent and spread of the petal lobes at

the corolla aperture. The Procrutes ANOVA analysis showed a strong and significant difference in shape between the two pollination strategies (R^2=0.687, p<0.001), and a negligible effect of error in the landmark positing (1.14% of the variation) and thus we used the mean of the two copies for the remaining analyses.

Variation in bill shape

The PCA shows that species tend to have different bill shapes (Procrustes ANOVA: R^2=0.5787, p<0.001; Figure 4). PC1 shows variation in bill curvature with species with curved bills on the left (such as *Eulampis jugularis*) and species with straight bills to the right, explaining 47.9% of the variation. PC2 explains 27.3% of the variation and shows mainly variation in bill thickness (i.e., distance between semi-landmarks at the top and bottom of the bill). PC3 explains 16.2% of the variation and represents variation in the position of the two landmarks at the base of the bill, which is where the bill connects to the head. We did not find a significant difference in bill shape between the species pollinating Gesneriaceae and the non-pollinator species (Procrustes ANOVA: p=0.37).

We also tested for differences in bill shape between sexes (dimorphism) by performing a Procrustes ANOVA with the sexes nested in species and found that the shape was significantly different between sexes (p<0.001), but this result did not hold when considering only pollinators of the Gesneriaceae (p=0.249). We therefore considered that each hummingbird species had only one bill shape in the remaining analyses and that hummingbird dimorphism was not a confounding variable in the present study. The error involved in landmark positioning was small (6.01%) and we used the mean of the two copies for the remaining analyses.

Bill corolla correlations: univariate comparisons.

We found significant associations between bill and flower characteristics for all comparisons, except for the regression of the flower length on bill curvature (Tables 3, A3, Figure 5). The interaction between the explanatory variable (bill trait) and the pollination strategy (specialist or generalist) of the plant species was found to be significant for the regressions of flower curvature on bill curvature and length (Table 3, Figure 5C, D). In both cases, specialists had a positive slope suggesting that an increase in bill length or bill curvature results in greater corolla curvature, whereas the trend was opposite for generalists (Table 4, Figure 5). The slope of the regression of corolla length on bill length was significant with a slope of 0.46 (Table 4), but the effect of pollination syndrome and the interaction between syndrome and bill length were not significant (Table 3).

Bill-corolla correlations: global shape comparison

To avoid singularity issues with the phylogeny due to the presence of the same plant species more than once in the dataset for the species pollinated by more than one hummingbird species, we performed phylogenetic two blocks partial least squares (p2B-PLS) analyses with all possible resampled datasets in which each plant species appeared only once (4 datasets for specialists and 2 for generalists). The p2B-PLS analyses showed a significant level of phylogenetic covariation between the corolla shape and the bill shape of their hummingbird pollinators for plant specialists (mean r-PLS=0.85, mean effect size=1.98, p-value range=0.005-0.024; Figure 6). The inspection of the shapes associated with the extremes of the regression axis between the first axes of the bill and corolla PLS further shows that straight bills are associated with straight corollas (upper right

of the ordination; Figure 6) and that curved bills are associated with curved corollas (bottom left of Figure 6). In contrast, the p2B-PLS was not significant for generalists (mean r-PLS=0.729, mean effect size=0.9148, p-value range=0.160-0.989).

DISCUSSION

Several studies have investigated the association between bill shape and floral shape, especially looking at organ length in plant species with specialized pollination systems (Agosta & Janzen, 2005; Dohzono *et al.*, 2011; Lunau, 2004; Maglianesi *et al.*, 2014; Temeles *et al.*, 2009; Van der Niet *et al.*, 2014). Here, we investigated the relationship between the shapes of corollas and that of the bill of their hummingbird pollinators using length and curvature measurements, but also more broadly by quantifying the covariation in shape between the corollas and the bills as characterized by geometric morphometrics.

Based on the comparison of the corolla shape and measurements of 18 species of Antillean Gesneriaceae species and that of the bill of their hummingbird pollinators (7 species), we found that the shape of the corollas and bills are correlated, but that the relationship differed according to the level of pollination specialisation of the plant species. For instance, the analysis of geometric morphometric data revealed that the global shape of the corollas was correlated with hummingbird bill shapes for hummingbird specialist species. Indeed, the p2B-PLS analysis suggested that curved flowers tend to be pollinated by hummingbird species that possess a curved bill and that straight flowers tend to be pollinated by hummingbirds with straight bills (Figure 6). In contrast, no significant global shape correlation was detected for generalist plant species. A similar trend was found by analysing curvature as the curvature of corollas and bills are positively correlated for

plants specialized for hummingbird pollination, but negatively so for generalist species (Figure 5). We found a significant relationship between corolla curvature and bill length, which differed according to the pollination strategy, although we note this relationship may be confounded by the strong correlation between bill length and bill curvature (r=0.742): birds with long bills tend to have curved bills.

The observation that the nature of the correlation between the shape of corollas and that of their hummingbird pollinators differ according to the level of pollination specialization may not be surprising given that hummingbirds represent only one of the various functional types of pollinators of generalist species. As such, the shape of generalist flowers could result from evolutionary trade-offs or particular selection pressures imposed by different pollinators (Aigner, 2001). There have been few clear demonstrations of such trade-offs on flower traits in pollination generalists (but see Muchhala 2007, Sahli & Conner, 2011), and while our results do not represent direct evidence, they are consistent with such an hypothesis, especially given that these pollination strategies have evolved repeatedly in the group (Joly *et al.*, 2018; Martén-Rodríguez *et al.*, 2010). However, trade-offs are not the only potential explanation; selection on specific floral traits by only particular pollinator species is also possible, as demonstrated in bee-pollinated *Medicago sativa* (Brunet et al. 2021). For instance, selection for corolla constriction in Antillean Gesneriaceae may be exerted mainly by hummingbirds to facilitate pollen removal and deposition, since exclusively bat-pollinated flowers do not have corolla constrictions. Finally, the corolla constriction of generalist species may alternatively represent a specialized trait that allows efficient pollination by both hummingbirds and bats (Martén-Rodríguez et al, 2009; Joly et al. 2018).

We also found a significant positive correlation between the length of corollas and the bill length of their hummingbird pollinators. In this case, the pollination strategy did not significantly affect the relationship, although there might be an effect of small sample size as a close inspection of the plot suggests that this trend is mostly observable for specialist species (Figure 5A). The slope of this relationship indicates that an increase of 1 cm in bill length is matched by an increase of 0.46 cm in corolla length (Table 4). One reason why this relationship departs from a slope of 1 could be that most hummingbirds pollinate plants with both long and short corollas (Figure 5). For example, the Antillean mango (*Anthracothorax dominicus*) with an average bill of 24 mm pollinates flowers with corollas that range from 19 mm (*Rhytidophyllum leucomallon*) to 29 mm (*Gesneria pedicellaris*). Departure from a perfect fit in terms of length has also been observed in several previous studies (Araujo & Sazima, 2003; Maglianesi *et al.*, 2014; Snow & Snow, 1980). But the fact that hummingbirds with long bills can pollinate flowers with longer corollas certainly contributes to a positive relationship between bill length and corolla length. Another source of variation is related to the capacity of hummingbirds to extend their tongues to reach deeper in corollas in order to access nectar (Stiles, 1975; Temeles, 1996). Indeed, according to our results, hummingbirds tend to visit Gesneriaceae flowers with corollas that are longer than their bills (Figure 5).

Hummingbirds have been shown to prefer small and wide flowers in some studies (Maglianesi *et al.*, 2015; Temeles *et al.*, 2009). Therefore, the linear relationship between corolla and bill length observed here and in previous studies (Cotton, 1998; Dalsgaard *et al.*, 2009; del Coro Arizmendi & Ornelas, 1990; Maglianesi *et al.*, 2014; Nattero & Cocucci, 2007) may be due to competition between hummingbirds that could lead to partitioning of floral resources according to their feeding efficiency and their ability to keep away other hummingbird species (Kodric-Brown *et al.*, 1984;

Maglianesi *et al.*, 2015; Temeles *et al.*, 2013). Consequently, competition could result in long-billed hummingbirds visiting flowers with longer corollas despite the availability of other floral resources. Indeed, the presence of other hummingbird-pollinated plants and other hummingbirds at the same location as the study species is known to contribute to niche partitioning in some studies (Tinoco *et al.*, 2017). In this study, the composition of hummingbird communities could be important in determining floral resources used in the Antillean islands with the greatest diversity of hummingbirds in terms of size and bill length (e.g., Hispaniola, Jamaica, and Puerto Rico). In contrast, the lower diversity of hummingbirds observed in Cuba (3 species) is less likely to play an important role in niche partitioning. Finally, the frequent correlation reported between corolla length and nectar volume (del Coro Arizmendi & Ornelas, 1990; Kodric-Brown *et al.*, 1984) and the reduced handling times by hummingbirds in flowers that better fit their bills (Maglianesi *et al.*, 2014) are probably important contributors to the positive association between the bill length of hummingbirds and the corolla length of the species they pollinate.

Previous studies that tested the relationship between the shape of corollas with those of the hummingbird bills have mostly used length measurements, although some have also investigated bill curvature and the volume of bills and corollas (Maglianesi *et al.*, 2014; Temeles *et al.*, 2009). We found that a morphometric approach provides substantial information on the nature of such morphological correlations in an evolutionary framework. We showed that corolla shape is correlated with the bill shape of their hummingbird pollinator, but not in the same way for specialist and generalist Gesneriaceae species. More precisely, we found that the curvature of corollas was positively correlated with the curvature of the bills of their hummingbird pollinators, but only for species specialized for hummingbird pollination and not for generalists. Such differences in correlation at a macro-evolutionary scale according to the level of pollination specialisation ask for

detailed pollination studies of the generalized species to better understand the forces and potential trade-offs that might be responsible for the global patterns of floral variation observed in Caribbean Gesneriaceae.

DATA AVAILABILITY

The data and scripts to reproduce the analyses presented in this study were deposited on FigShare: doi 10.6084/m9.figshare.16866799.

AUTHOR CONTRIBUTIONS

JF and SJ designed the study. JF, JLC and SMR collected the data. JF and SJ analyzed the data. JF wrote the initial version of the manuscript and all authors contributed to the writing of the final version.

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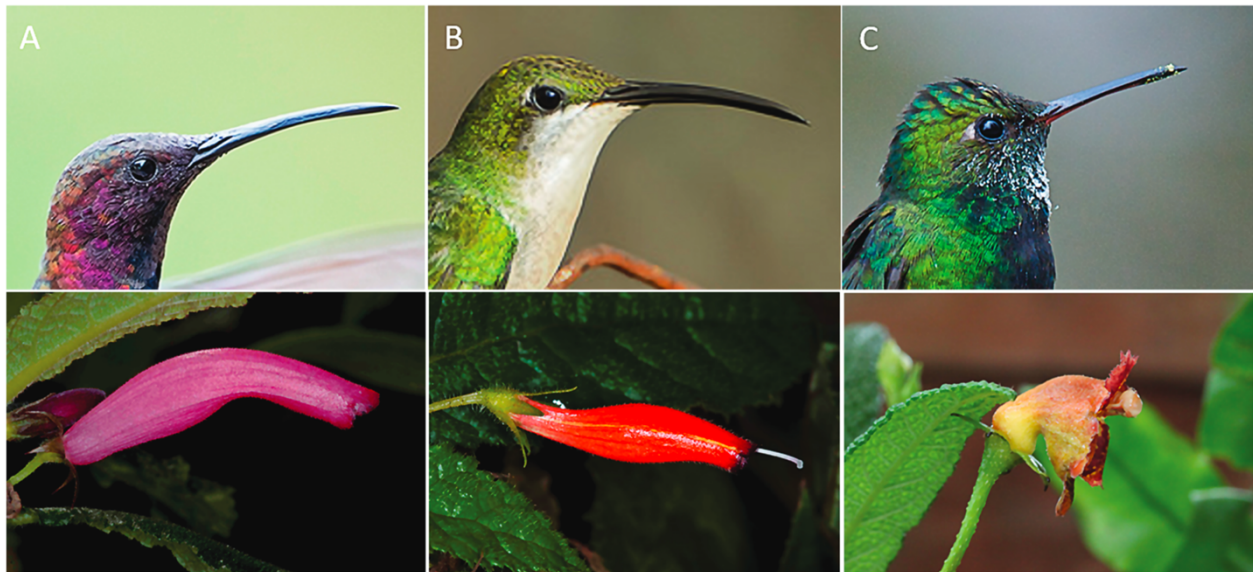
FIGURES

Figure 1. Profile pictures of the bill of different species of hummingbirds of the Carribean showing the variation of bill shape between species, and profile view of the corolla of the Gesneriaceae they pollinate. (A) *Anthracothorax mango* pollinates *Gesneria acaulis*, (B) *Anthracothorax dominicus* pollinates *Gesneria pedicellaris* and (C) *Chlorostilbon swainsonii* pollinates *Rhytidophyllum vernicosum* Photo credits: Hummingbirds: Rafy Rodriguez, Gesneriaceae: John J Clark and Simon Joly.
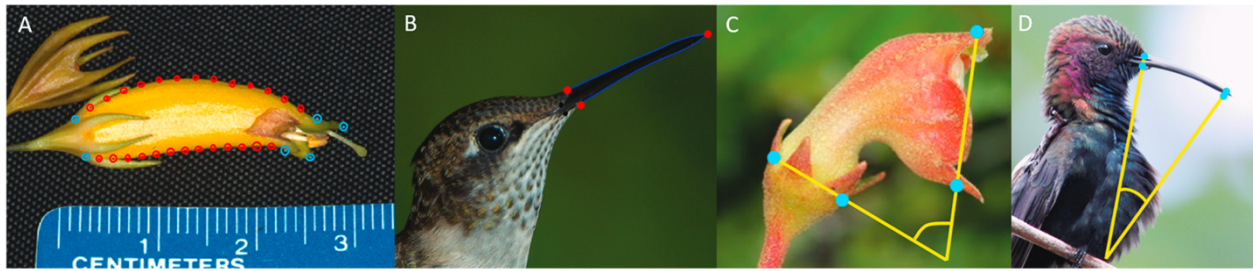
Figure 2. A) Example of landmark (blue dots) and semi-landmarks (red dots) positioning for the geometric morphometric analysis of floral shape ; B) Example of landmark (red dots) and curve for semi-landmarks (blue line) positioning for the geometric morphometric analysis of bill shape ; C) Example of measurement of corolla curvature with landmarks (base and opening of the corolla) of the geometric morphometric data (blue dots) ; D) Example of the measurement of bill curvature with landmarks (base of the bill) and semi-landmarks (next to the tip of the bill) (blue dots).
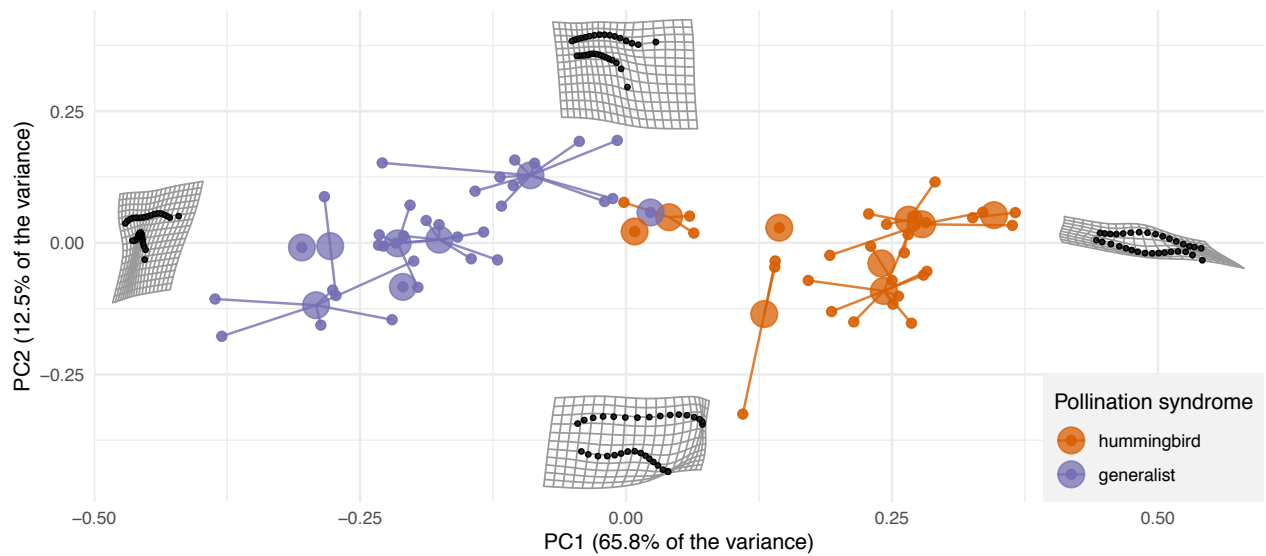
Figure 3. Principal Component Analysis of floral traits that determine corolla shape. Large dots represent the means for each species and they are connected by lines to small dots that represent the floral shapes of the individuals belonging to each species. Thin-plate spline deformation grids show corolla shape variation among the principal components, plus or minus 2 standard deviations from the mean shape.
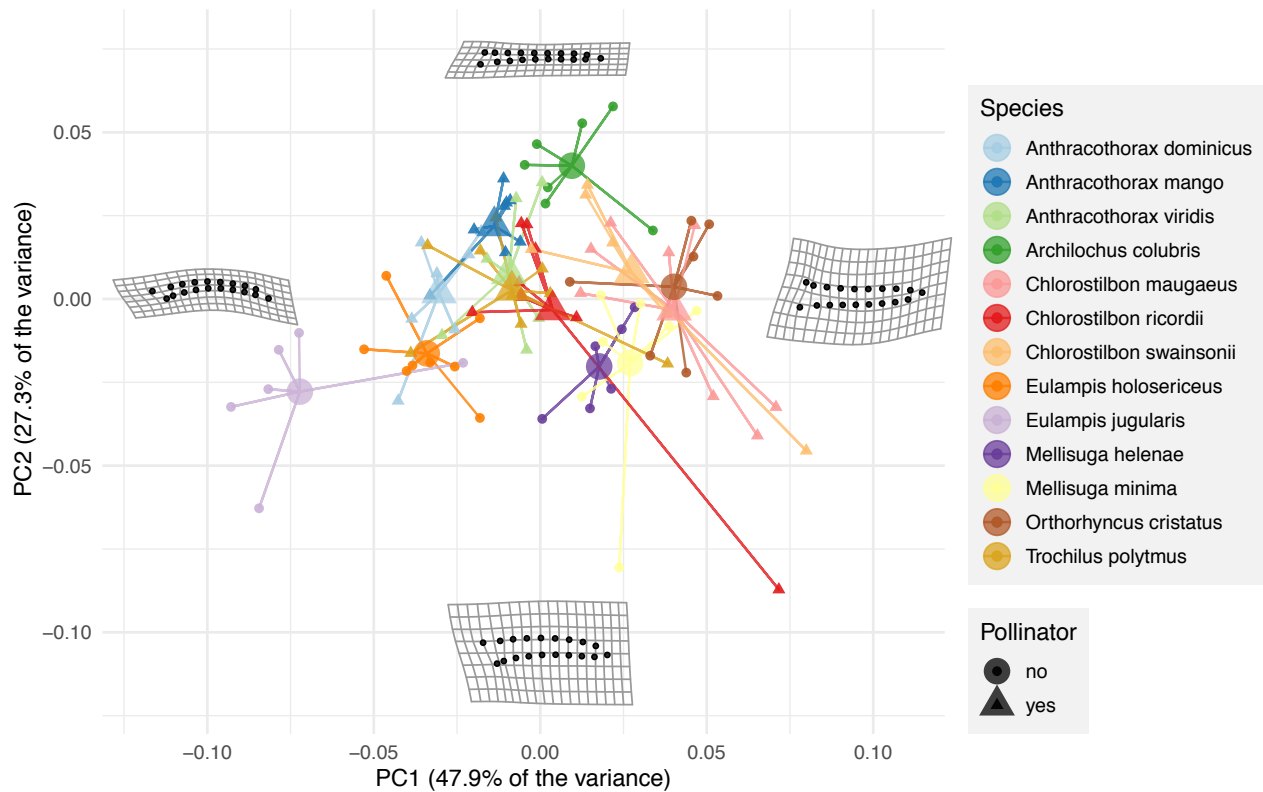
Figure 4. Principal Component Analysis of bill shape traits of hummingbirds from the Greater Antilles, with confirmed pollinators highlighted by a triangle shape. Species are differentiated by colors. Large dots represent the means for each species, which are connected by lines to small dots that represent the bill shapes of the individuals belonging to each species. Thin-plate spline deformation grids show bill shape variation among the principal components, plus or minus 2 standard deviations from the mean shape.
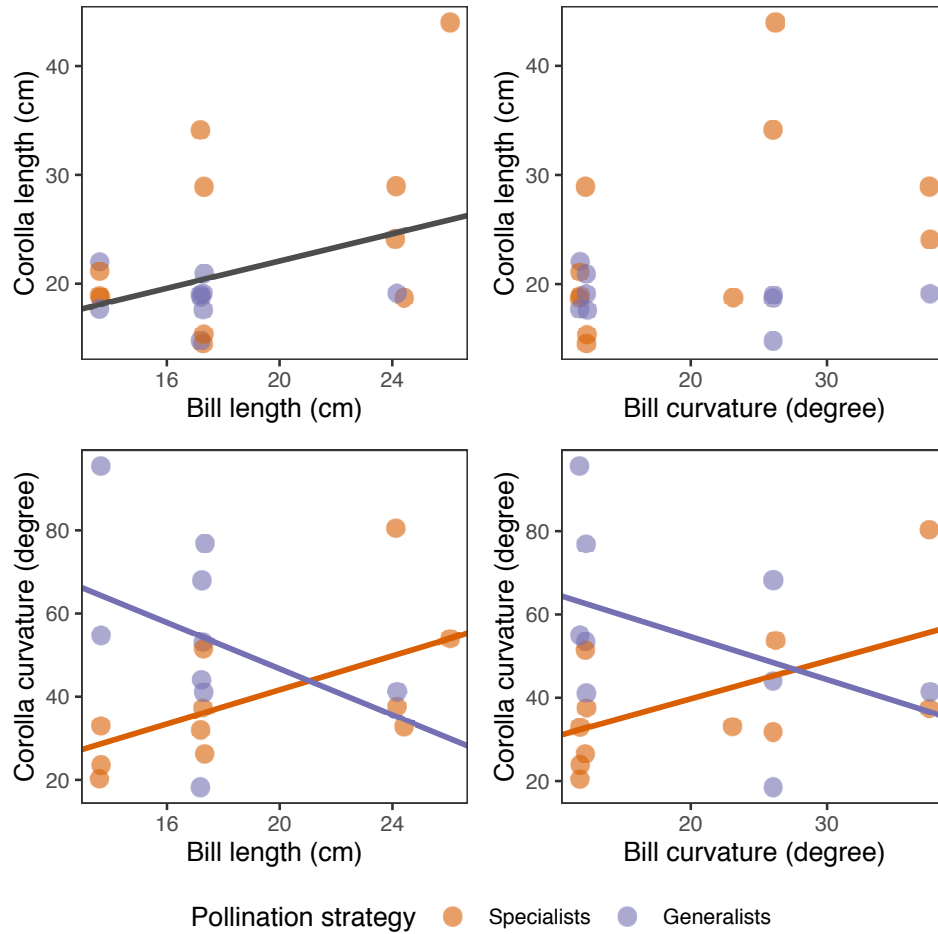
Figure 5. Plots showing the relationship between the top corolla length or the corolla curve and the length and the curvature of their hummingbird pollinators. Slopes are provided when found significant, either for the full data or independently for specialists and generalists when the interaction with the pollination strategy was significant (see Tables 3, 4). Random noise was added to the points (jitter) to facilitate visualization.
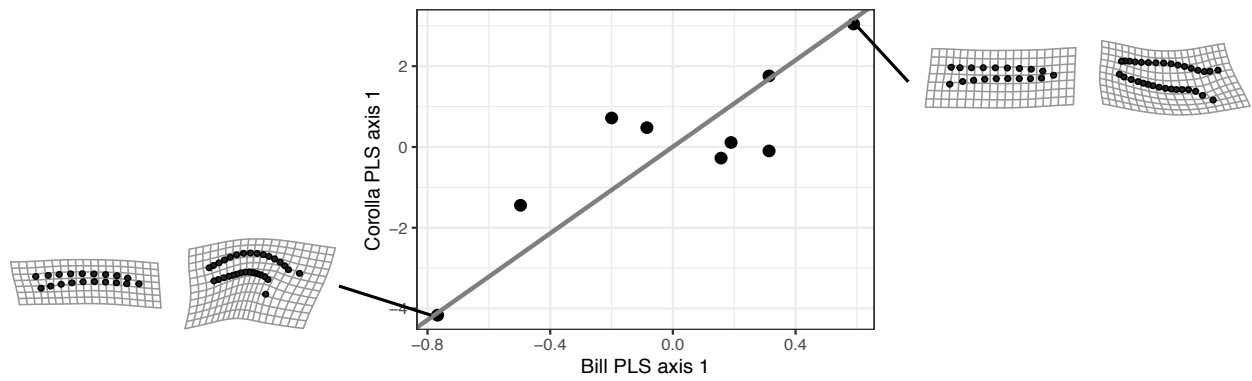
Figure 6. Ordination of the phylogenetic two blocks partial least squares (p2B-PLS) illustrating the phylogenetic morphological covariation between the shape of the corolla and the shape of their hummingbird pollinators as characterized by geometric morphometrics. This specific ordination includes the *Gesneria citrina - Anthracothorax viridis* and the *G. pedicellaris - Chlorostilbon swainsonii* comparisons (see Methods). The covariation in shape is illustrated using warpgrids with deformation from the mean corolla and bill shapes at the extremes of the regression between the first partial least squares axes (see lines).

Table 1. Species of Gesneriaceae included in this study, pollination mode, floral trait measurements (± SD), confirmed hummingbird pollinator(s), and island of occurrence. Abbreviations for the islands: Puerto Rico: PR, Cuba: C, Jamaica: J, Hispaniola: H and the Lesser Antilles: LA.

Species	Pollination mode	Mean Top Length (mm)	Sample size (for length)	Curvature	Hummingbird Pollinator	Island of occurrence
Gesneria acaulis	Hummingbird	44 ± 0.52	2	53.82 ± 5.92	*Anthracothorax mango*	J
Gesneria citrina	Hummingbird	18.7 ± 3.73	3	32.85 ± 11.13	*Anthracothorax viridis, Chlorostilbon maugaeus*	PR
Gesneria cubensis	Hummingbird	24.1 ± 5.78	5	-	*Anthracothorax dominicus*	C, H
Gesneria cuneifolia	Hummingbird	21.1 ± 1.32	6	20.29 ± 12.95	*Chlorostilbon maugaeus*	PR
Gesneria pedicellaris	Hummingbird	28.9 ± 0.18	2	37.48 ± 22.93	*Anthracothorax dominicus, Chlorostilbon swainsonii*	H
Gesneria pulverulenta	Hummingbird	14.5 ± 0.42	3	26.45 ± 1.21	*Chlorostilbon swainsonii*	H
Gesneria purpurascens	Hummingbird	34.1 ± 6.27	3	31.68 ± 19.76	*Chlorostilbon ricordii*	C
Gesneria quisqueyana	Mixed-pollination	19.9	1	39.12 ± 1.27	*Chlorostilbon swainsonii*	H
Gesneria reticulata	Hummingbird	18.9 ± 2.42	3	23.78 ± 10.80	*Chlorostilbon maugaeus*	PR, C, H
Gesneria sintenisii	Mixed-pollination	22	1	95.66 ± 2.87	*Chlorostilbon maugaeus*	PR
Gesneria viridiflora	Mixed-pollination	19 ± 2.94	10	68.05 ± 12.39	*Chlorostilbon ricordii*	C
Rhytidophyllum auriculatum	Mixed-pollination	17.7 ± 1.38	7	54.79 ± 8.04	*Chlorostilbon maugaeus*	PR, H

Rhytidophyllum berteroanum	Hummingbird	15.4 ± 1.43	4	51.36 ± 13.13	*Chlorostilbon swainsonii*	H
Rhytidophyllum exsertum	Mixed-pollination	18.7 ± 1.66	14	43.94 ± 13.47	*Chlorostilbon ricordii*	C
Rhytidophyllum grandiflorum	Mixed-pollination	20.9	1	53.22 ± 5.23	*Chlorostilbon swainsonii*	H
Rhytidophyllum leucomallon	Mixed-pollination	19.1 ± 2.83	4	41.30 ± 13.95	*Anthracothorax dominicus, Chlorostilbon swainsonii*	H
Rhytidophyllum minus	Mixed-pollination	14.8 ± 2.40	4	18.32 ± 1.78	*Chlorostilbon ricordii*	C
Rhytidophyllum vernicosum	Mixed-pollination	17.6 ± 3.68	2	75.95 ± 2.22	*Chlorostilbon swainsonii*	H

Table 2. Data for the hummingbird species studied (weight, bill length, bill curvature with standard deviation, presence and type of sexual dimorphism, islands of occurrence, if it is a confirmed pollinator of Gesneriaceae, and number of photographs studied). Abbreviations for the islands: Puerto Rico: PR, Cuba: C, Jamaica: J, Hispaniola: H and the Lesser Antilles: LA. Bill size and weights of all the species come from Brown & Bowers (1985).

Species (Common name)	Scientific name	Weight (g)	Bill length (mm)	Curvature	Dimorphism	Island of occurence	Pollinator confirmed	Number of photographs
Ruby throated hummingbird	*Archilochus colubris*	3.19	17.96	14.13 ± 6.21	Plumage	PR, H, C	no	7
Bee hummingbird	*Mellisuga helenae*	2.60	10.76	23.76 ± 10.08	Plumage and size	C	no	6
Green mango	*Anthracothorax viridis*	6.60 ± 0.4	24.40 ± 1.17	23.10 ± 11.39	Bill, plumage and size	PR	yes	6
Jamaican mango	*Anthracothorax mango*	7.81 ± 0.67	26.03	26.24 ± 14.09	Bill, plumage and size	J	yes	10
Purple throated carib	*Eulampis jugularis*	8.67 ± 0.56	23.59	51.17 ± 20.14	Bill, plumage and size	LA, PR	no	6
Puerto rico emerald	*Chlorostilbon maugaeus*	2.93 ± 0.2	13.62 ± 0.6	11.82 ± 8.67	Bill, plumage and size	PR	yes	8
Hispaniolan emerald	*Chlorostilbon swainsonii*	4.85	17.30	12.32 ± 12.34	Bill, plumage and size	H	yes	6
Red billed streamertail	*Trochilus polytmus*	4.10	19.80	32.86 ± 15.51	Bill, plumage and size	J	yes	10
Green throated carib	*Eulampis holosericeus*	5.60 ± 0.40	22.74 ± 2.20	46.09 ± 9.21	Bill, plumage and size	LA,PR	no	8
Antillean crested hummingbird	*Orthorhyncus cristatus*	2.71 ± 0.18	10.72 ± 1.18	14.43 ± 8.53	Plumage and size	LA,PR	no	7
Cuban emerald	*Chlorostilbon ricordii*	4.23	17.20	26.03 ± 12.68	Bill, plumage and size	C	no	9
Vervain hummingbird	*Mellisuga minima*	2.43 ± 0.10	10.45	20.04 ± 11.50	Size	H,J	yes	7

Antillean mango	*Anthracothorax dominicus*	5.66 ± 0.41	24.13 ± 0.75	37.49 ± 14.09	Bill, plumage and size	H, PR	yes	7

Table 3. Model comparison for linear regressions of univariate characters (corolla length, corolla curvature) of Antillean Gesneriaceae. The best model for each correlation is indicated in bold (lowest Akaike Information Criterion, AIC). See also Table A3 for the results with the bottom corolla length.

Response variable	Correlation tested	Models	df	lnL	AIC
Corolla length (Top)	Corolla length ~ Bill length	Corolla length ~ 1	2	-63.222	132.434
		Corolla length ~ Bill length	**3**	**-61.010**	**131.007**
		Corolla length ~ Bill length + strategy	4	-60.960	133.903
		Corolla length ~ Bill length + strategy + bill length:strategy	5	-60.111	135.201
	Corolla length ~ Bill curvature	**Corolla length ~ 1**	**2**	**-56.400**	**116.794**
		Corolla length ~ Bill curvature	3	-56.385	118.771
		Corolla length ~ Bill curvature + strategy	4	-56.342	120.684
		Corolla length ~ Bill curvature + strategy + bill curvature:strategy	5	-56.327	122.654
Corolla curvature	Corolla curvature ~ Bill length	Corolla curvature ~ 1	2	-88.450	180.899
		Corolla curvature ~ Bill length	3	-88.300	182.600
		Corolla curvature ~ Bill length + strategy	4	-86.880	181.761
		Corolla curvature ~ Bill length + strategy + bill length:strategy	**5**	**-84.462**	**178.924**
	Corolla curvature ~ Bill curvature	Corolla curvature ~ 1	2	-88.464	180.928
		Corolla curvature ~ Bill curvature	3	-88.422	182.844
		Corolla curvature ~ Bill curvature + strategy	4	-87.234	182.469
		Corolla curvature ~ Bill curvature + strategy + bill curvature:strategy	**5**	**-84.088**	**178.176**

Table 4. Model parameters of the best variables for the univariate floral characters of Antillean Gesneriaceae. The dash marks indicate that these parameters were not found to be significant in the model (see Table 3 for the model comparisons). All models were fitted by restricted maximum likelihood (REML) and standard errors around the estimates are provided where appropriate.

Response variable	Independent variable	Intercept	Slope	Strategy	Interaction	Lambda
Corolla length	Bill length	12.69 ± 5.27	0.46 ± 0.22	-	-	0.84
Corolla length	Bill curvature	-	-	-	-	-
Corolla curvature	Bill length	0.76 ± 22.58	2.04 ± 1.12	101.5 ± 41.17	-4.82 ± 2.30	0.29
Corolla curvature	Bill curvature	21.50 ± 12.56	0.91 ± 0.51	53.75 ± 18.25	-1.94 ± 0.80	0.27