Plant-pollinator specialization: Origin and measurement of curvature

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#### Abstract

A feature of biodiversity is the abundance of curves displayed by organs and organisms. An example is the curvature of flowers and pollinator mouthparts (e.g. hummingbird bills) along the dorsiventral plane. This is a widespread, convergent trait with important ecological and evolutionary implications. Pollination ecologists are concerned with flower-pollinator curvature because it appears to be a derived trait associated with specialization, competition, and species co-existence. In this review we summarize and evaluate the four methods historically used to measure curvature in pollination systems and suggest a clarification of its general definition using concepts of differential geometry. Intuitively, curvature is the degree to which a line is not straight, or more formally, the rate at which the unit derivative changes direction with respect to arc length. To apply this definition we suggest a protocol wherein a line is regressed against landmarks placed on an image of a curved organ or organism, then curvature is computed at many points along the fitted line and the sum taken. The protocol is demonstrated by studying the development of nectar spur curvature in *Epimedium* (Berberidaceae). By clarifying the definition of curvature, the language of comparative morphology is made more precise. In this study we found *Epimedium koreanum* to have an order of magnitude greater curvature than the closely related *E. violaceum* at the early stages of flower development. That is, *E. koreanum* had greater total degrees of rotation along the arc of the nectar spur. The functions used to quantify floral curvature in this study are available as an R package ‘curvr’. The major advantages of this method are 1) increased precision of measurement, and 2) improved precision of terminology in biology by adopting the existing mathematical terms for studying line-curves.

#### The ecology of flower-pollinator curvature

*“We are beginning to understand why some hummingbird bills are long, whereas others are short, and why some hummingbird flowers are wide, whereas others are narrow. Now, why are bills of some hummingbirds and the tubes of the flowers they visit curved?”* – Temeles ([1996](#ref-temeles_1996)).

At the center of plant-pollinator diversification is a remarkable variety of floral form. The notion that plant communities experience selection to reduce interspecific mating (“floral isolation”, Grant, [1949](#ref-grant_1949)) points to the importance of floral diversity in initiating and reinforcing reproductive isolation (Armbruster and Muchhala, [2009](#ref-armbruster_2009)). For example, in the rapid radiation of Andean *Centropogon* C.Presl (Campanulaceae), competition for pollination led to the divergence of floral traits associated with bat and hummingbird pollination (Lagomarsino and Muchhala, [2019](#ref-lagomarsino_2019)). In the case of South African *Lapeirousia* Pourr. (Iridaceae), geographic variation in floral tube length has initiated reproductive isolation between morphs with short and long corolla tubes, despite sharing the same fly pollinator (Minnaar et al., [2019](#ref-minnaar_2019) ). While patterns of plant-pollinator evolution point to both contemporaneous and asymmetrical co-adaptation (Cardinal and Danforth, [2013](#ref-cardinal_2013); Tripp and McDade, [2013](#ref-tripp_2013)), floral morphology can both be the cause and result of plant-pollinator diversification (Kay and Sargent, [2009](#ref-kay_2009); Niet and Johnson, [2012](#ref-vanderniet_2012); Ollerton, [2017](#ref-ollerton_2017)).

   Flower-pollinator curvature as viewed from the side (dorsiventral plane), has been a trait of special interest since the post-Darwin era of pollination ecology. However, floral curvature has origins that likely precede any particular ecological function. Instead, curved flowers (e.g. nectar spurs) might develop within buds when constrained for space. That is, during bud development nectar spurs elongate and curve when met with resistance from the enclosing bud tissue. Following bud opening flowers may straighten but retain some degree of curvature at maturity. Consequently, like floral tube length (e.g. Nilsson, [1988](#ref-nilsson_1988); Hodges and Arnold, [1995](#ref-hodges_1995)), there can be positive selection for curvature when it increases the complexity of nectar extraction and mechanical interaction between the anthers and the body of the pollinator (Young, [2008](#ref-young_2008); Collins, [2008](#ref-collins_2008)).

   A further consequence of floral curvature is pollinator partitioning. In making pollinator observations of the Cape flora, Scott-Elliott ([1890](#ref-scott-elliot_1890)) noticed that the flowers of *Leonotis ocymifolia* (Burm.f.) Iwarsson (Lamiaceae) visited by *Nectarinia* Illiger (Nectariniidae) sunbirds were “curved with the same curvature as that of the bird’s beak.” (p. 272). Robertson ([1889](#ref-robertson_1889)) insightfully notes that the curved nectar spurs of *Viola* L. (Violaceae) “serves to limit the insect visits much more than the mere length of the spur.” (p. 172). From these early observations, curvature has been synonymous with specialization; we expect curvature to limit the range of functional taxa in a plant-pollinator mutualism and strengthen interactions between the existing participants. Stiles ([1975](#ref-stiles_1975)) first posited that neotropical *Heliconia* L. (Zingerberales) partition hummingbird (Trochilidae) visitation by flower-bill curvature, and that specialization by curve-billed hummingbirds allow co-existence within the species-rich *Heliconia* clade. Subsequent research supports this hypothesis (Maglianesi et al., [2014](#ref-maglianesi_2014)): along the slopes of the Central Cordillera (Costa Rica), the degree of flower-hummingbird bill curvature is proportional to plant-pollinator interaction strength (Dehling et al., [2014](#ref-dehling_2014)) and extent of specialization (*sensu* Blüthgen et al., [2006](#ref-bluthgen_2006)). In addition to interspecific partitioning of resources, many hummingbirds exhibit sexual dimorphism in bill shape - females have greater bill curvature than males and forage for nectar from curved flowers (Temeles et al., [2005](#ref-temeles_2005), [2010](#ref-temeles_2010)). Explanations for this pattern range from reduced competition for nectar resources between sexes (Paton and Collins, [1989](#ref-paton_1989); Temeles et al., [2010](#ref-temeles_2010)) to selection for mechanically superior bill shapes during male-male fighting for territory (Rico-Guevara and Araya-Salas, [2014](#ref-rico_2014)). More recently the scope of plant-hummingbird research has expanded to address the biogeography of curvature. As predicted by Stiles ([2004](#ref-stiles_2004)), Maglianesi ([2015a](#ref-maglianesi_2015_b)) and Sonne ([2019](#ref-sonne_2019)) found plant-hummingbird curvature to be most prevalent in the lowland environments of the neotropics. In this case, curvature is a form of character displacement evolving in lowland habitats experiencing relatively higher competition than the adjacent Andes mountains (Stiles, [2004](#ref-stiles_2004); Graham et al., [2009](#ref-graham_2009)). Furthermore, because plant-hummingbird morphology becomes more specialized at lower latitudes (Sonne et al., [2020](#ref-sonne_2020)) and hummingbirds with curved bills are predominately neotropical, we might expect plant-hummingbird curvature to have a predictable continental distribution.

   While curvature mediates specialization in plant-hummingbird systems, in other nectivorous bird groups curvature has a different ecological role. In plant-passerine systems, curvature is more prevalent in pollinators than in flowers. Straight flowers do not necessarily exclude pollination by curve-billed birds; for example, the straight, tubular flowers of African *Aloe* L. (Asphodelaceae) are pollinated by curve-billed sunbirds (Paton and Collins, [1989](#ref-paton_1989)), and the small campanulate flowers of *Vaccinium* L. (Ericaceae) are pollinated by the Hawaiian honeycreeper *Drepanis coccinea* Forster (Fringillidae, Carothers ([1982](#ref-carothers_1982))). For these passerine clades, a dietary shift to nectivory may drive the evolution of bill curvature because (ancestral) insect-pollinated plants require perching at angles not directly facing the flower opening (Paton and Collins, [1989](#ref-paton_1989)). A comparison of honeyeaters (Meliphagidae; predominately Australasian), sunbirds (Africa, Australasia), Hawaiian honeycreepers, and hummingbirds (Nearctic, Neotropic) demonstrates that bill curvature is widespread in all groups but the latter (Paton and Collins, [1989](#ref-paton_1989)). A notable difference being that hummingbirds can manoeuvre adeptly, while other birds perch while probing for nectar. For these plant-passerines systems, selection is largely acting on the pollinator (i.e. bird bill): insectivorous birds evolve curved bills to feed from plants with straight, tubular flowers, and in only some cases does reciprocal evolution produce curved flowers e.g. sunbird-pollinated *Streptocarpus dunnii* Mast. (Gesneriaceae, Hughes et al. ([2007](#ref-hughes_2007))). It is worth noting that in landbirds, the evolution of bill shape is coupled with skull shape (Bright et al., [2016](#ref-bright_2016); Navalón et al., [2020](#ref-navalon_2020)). Therefore, in certain passerine pollinator clades (e.g. Hawaiian honeycreepers), the rapid diversification of bill shape is influenced not only by flower eco-morphology, but also by any ecological factors that influence bodysize (Navalón et al., [2020](#ref-navalon_2020)).

   Floral diversity contributes to floral isolation and diversification in the angiosperims (Kay and Sargent, [2009](#ref-kay_2009); Armbruster and Muchhala, [2009](#ref-armbruster_2009); Vamosi et al., [2018](#ref-vamosi_2018)). Similarly, dietary specialization within pollinator clades has contributed to the diversification of mouthpart morphology (Weinstein and Graham, [2017](#ref-weinstein_2017); Maruyama et al., [2018](#ref-maruyama_2018)). In both cases, curvature is a widespread feature of morphological diversity. Therefore, to synthesize our knowledge of curved plant-pollinator systems, curvature is a concept that needs an exact definition and method of measurement. In the following section we summarize the approaches to measuring curvature within the field of pollination ecology, identify strengths and shortcomings, and offer a solution with the aim of improving the precision with which curvature is measured. Although this review is motivated by the problem of measuring curvature in plant-pollinator systems, the solution is general to any biological form modelled as a line curve: and we hope this case is made in the demonstration to follow.

#### Summary of the literature: history of measuring curvature in pollination ecology

We searched the scientific literature for studies focusing on or considering the curvature of flowers and their pollinators - a trait commonly measured as a proxy for specialization. We make the distinction between measuring curvature (e.g. of petals) in the dorsiventral plane versus the curvature of surfaces. While dorsiventral images are analysed for line-curvature, images of specimens in the transverse plane can be used to analyse surface (Gaussian) curvature (Nath et al., [2003](#ref-nath_2003); Coen and Rebocho, [2016](#ref-coen_2016)). The methods used in the latter are relatively more complex, and perhaps because of this, comparatively well-defined. At present, surface curvature has yet to be considered in the context of pollination, and is probably of limited importance: floral tubes are generally circular in cross-section and surface curvature takes the form of a simple or flared cylinders, and complex and mathematically interesting curved surfaces such as saddle-shapes, are absent. Furthermore, because line and surface curvature are related mathematical concepts, it will benefit pollination research to clarify the simplest case (lines), with the goal of generating interest in related ideas including the curvature of surfaces.

   The literature was sourced by querying Web of Science and Google Scholar for a topic search of (curv\*) AND (pollinat\*) AND (flower OR corolla OR \*bird OR \*bee OR moth OR \*fly). The initial search returned over 300 studies that were then screened for those that measured flowers and/or animal mouthparts (e.g. bird bills, moth tongues). We sorted studies based on the criteria that 1) the study focused on pollination, including qualitative measures of curvature and 2) the study measured flower or animal (mouthpart) curvature for other reasons, but measurements must be quantitative. Under these criteria, 40 studies were identified to have used some form of curvature metric (Table 1). An additional 17 studies discussing flower-animal curvature, but not related to pollination (e.g. frugivory, ornamental horticulture, taxonomy) are included in Table S1. There were numerous studies of plant-animal morphology that did not address curvature - these were omitted.

   In our survey, the first dedicated discussion of dorsiventral curvature in plant-pollinator interactions begins with Hainsworth ([1973](#ref-hainsworth_1973), in reference to *Heliconia* and hermit hummingbirds). Curvature in pollination ecology is first empirically studied by Feinsinger ([1978](#ref-feinsinger_1978)), though methods for measuring curvature of bird appendages outside of a pollination context can be found much earlier (Baldwin et al., [1931](#ref-baldwin_1931)). We identified six common approaches to measuring curvature in pollination systems. These are:

1. *qualitative description*, e.g. “very curved”, “less curved”, but these are generally no longer used;
2. the *arc:chord* (maxillary index) method which measures curvature as a ratio of two lines: a straight line (chord) from tip to base (of the flower or mouthpart, e.g. bird bill) and a line that traverses a path along the arc of the flower/bill (Figure 1);
3. the *mandibular index* method which defines curvature as a ratio of two lines: a straight line from base to tip and a perpendicular line that measures the depth of the flower/bill. This method is another form of the *arc:chord* method because for a given chord length, the length of the perpendicular line will be proportional to the arc length;
4. the *angle of deflection* (angle of declension) method which considers curvature as the angle between the base of the flower/bill and its tip;
5. the *inverse radius* method which approximates the entire length of the flower/bill as a segment of a circle. As pointed out by Temeles ([2009](#ref-temeles_2009)), the *inverse radius* method is another form of the *angle of deflection* method because the radius of a circle can be calculated from the length and angle of a line that passes through it (demonstrated by Bell, [1956](#ref-bell_1956), Figure S1);
6. *geometric morphometrics*, which quantifies shape as a configuration of homologous points (landmarks) existing on a coordinate plane (Figure S2).

The strength of the *arc:chord* and *mandibular index* methods are their portability and accessibility. These measurements can be taken in the field, or used easily from photographs. The methods are intuitive and in the simplest case, require only a ruler, string, and protractor. However, these methods have some conceptual flaws (discussed in Berns and Adams, [2010](#ref-berns_2010)). Because these methods approximate total curvature and not point-wise curvature, specimens with the same curvature values cannot be inspected for local features that may distinguish them. For the *inverse radius* method, a curve is approximated with the segment of a circle. This method is insufficient for any flower and mouthpart shapes that deviate from having constant curvature e.g. nectar spurs of *Delphinium* L. (Ranunculaceae). Similarly, the *angle of deflection* is not sensitive to local features along the length of the flower/bill - only the start and end points are considered in the calculation.

   An additional problem is that terminology is inconsistent between authors. For example, the *arc:chord* method is also called the *maxillary index*, while the *angle of deflection* method is sometimes referred to as the *angle of declension* method. Furthermore there is variation in how the methods are applied. In the application of the *mandibular index* one study adjusted for bill length while a subsequent study did not (Table 1). Many studies create their own terminology for the concept of arc length: the length of a curve between two points. Most studies define their own terms for measuring and reporting curvature without reference to previous studies that have studied curvature in similar systems. This creates uncertainty about how to compare and convert metrics used between studies. We believe these problems could be remedied by referring to the mathematical literature for the derivation and definition of curvature and related concepts.

   Starting with Berns and Adams ([2010](#ref-berns_2010)) geometric morphometrics emerges more recently in the pollination literature. In general, the field of morphometrics is concerned with the covariance of shape and associated or causal variables (Bookstein, [1991](#ref-bookstein_1991); MacLeod, [2002](#ref-macleod_2002)), e.g. how flower shape might covary with the identity of the most effective pollinator. This approach has steadily gained in popularity due to its mathematical rigour, reproducibility, and the appealing visual representations of shape comparisons e.g. geographic co-variation of flower shape and pollinator communities (Gómez et al., [2009](#ref-gomez_2009)), and functional bill diversity in waterfowl (Olsen, [2017](#ref-olsen_2017)). We highlight some of the broad features of morphometrics in order to introduce relevant concepts, but recommend the concise and authoritative introduction by Webster and Sheets ([2010](#ref-webster_2010)).

   In *traditional morphometrics* one-dimensional measurements - such as length, width, angle - are the primary data used to quantify shape. *Geometric morphometrics* (GM) improves these analyses by placing specimens in a Cartesian coordinate system and assigning landmarks at homologous points. By doing this, GM more completely captures the geometry of a specimen. Within GM there exist two related approaches: *Outline based-* and *landmark based geometric morphometrics*.

   A GM protocol for a 2-D object begins by placing the specimens on an *xy* grid and assigning landmarks to locations on the specimen that are topologically or biologically homologous (see considerations for landmark selection in Bookstein, [1991](#ref-bookstein_1991)). The set of landmarks representing the shape of an organism is a ‘landmark configuration’. In a comparative study, the samples are overlaid so that their shape information is isolated from their orientation, location, and size. This is done using a least-squares type protocol, most commonly the Generalized Procrustes Analysis (GPA). GPA-adjusted landmark configurations hereafter exist in a multidimensional shape space defined by the number of landmarks and spatial dimensions implemented. Each landmark configuration contains unique information about the specimen’s shape, and as such, occupies a unique position in the corresponding shape space. These configurations are then “projected” onto a simpler Euclidian space, similar to the reduction of a spherical Earth onto a two-dimensional map (Webster and Sheets, [2010](#ref-webster_2010)). From here, familiar statistical procedures (e.g. PCA) can be performed to quantify variation in landmark configurations (shape) between samples.

   This is giant leap forward for morphological studies because GM is a complete protocol for measuring, quantifying, and comparing shapes with high precision, as well as the covariation of these shapes with ecological variables of interest. Because GM has a traceable mathematical lineage (Bookstein, [1991](#ref-bookstein_1991)), its vernacular is well-defined and used consistently between practitioners.

   However, the limitation of GM in quantifying curvature is that this method is concerned with analyzing configurations of landmarks, i.e. the entirety of a shape summarized as a set of *xy* coordinates. Once the specimen has been reduced to a landmark configuration it exists as a point in shape space - this loss of information was recognized by the early developers of GM (Bookstein, [1978](#ref-bookstein_1978)). Parsing segments of landmark configurations for separate analyses (e.g. for curvature) is not currently part of the geometric morphometrics toolkit (see section 4 for a discussion of the role of curvature in GM). Therefore, studies that have used this technique to analyse biological forms are able to compare shapes in their entirety, but are ultimately limited to making descriptive statements about how segments of shapes appear to have different curvatures (e.g. Berns and Adams, [2013](#ref-berns_2013)).

#### What is curvature?

Reviewing the literature leads us to ask, “what is curvature?”. Within pollination ecology there are at least four metrics in use, with few references to their origins or the meaning of the associated units. In related fields, e.g. in plant physiology there have been uses of a point-wise defintion of curvature resembling that used in differential geometry (Castle, [1962](#ref-castle_1962)). However, as in pollination ecology, references to the mathematical literature are missing. Therefore, we propose turning to the field of geometry in order to develop the concept of curvature starting from first principles. There, we again find several definitions resulting from a history of independent derivations (reviewed in Coolidge, [1952](#ref-coolidge_1952); Bardini and Gianella, [2016](#ref-bardini_2016)). Nonetheless these definitions share a conceptual theme; curvature is a local property that can measured point-wise on a line. This concept is fundamentally different from those used in pollination ecology, where curvature is single property of an entire shape. Here we follow the conventions of Casey ([1996](#ref-casey_1996)) and Rutter ([2000](#ref-rutter_2000)) and present a definition of curvature that is tractable for analyzing biological shapes.

   Intuitively, when a line deviates from being straight we say it is curved, the extent to which it is not straight is its curvature. More technically, a line deviates from being straight when its slope (i.e. the first derivative) changes direction - this is represented here by the rotating tangent vectors , , , in Figure 2. Therefore, curvature can be thought of as the rate of change in the tangent as we move across the curve. Hence, the tangents of a straight line will have the same direction everywhere and a curvature of zero, whereas the tangents of the curve shown in Figure 2 will change direction and have a non-zero curvature.

   To formalize these concepts mathematically we begin by considering an ordinary function of the form , where specifies one value of for each value of . Biological curves, however, often loop back on themselves (e.g. spirals) and are better described by parametric fuctions that allow the curve to have multiple values for a single . Parametric functions use a ‘hidden’ variable that determines the values of and independently. Here, we use the parameter variable arc length, , along the curve. We can then express a position vector as a function solely of arc length, . Specifically, using vector notation we have:

Here is shorthand for which indicates that our position on the curve is determined by the length of the segment . Although we could parameterize a curve by many potential parametric variables, arc length is a convenient choice because it allows us to move along the curve at even increments, which we denote as . This proves useful when taking repeated, equally-spaced measurements along a curve, such as curvature.

   As we are interested in the derivative properties of our arc-length parameterized curve, we can differentiate with respect to arc length in the following way (using the formal definition of the derivative):

This produces a tangent function giving the first derivative of the parametric equation . The tangent , represented by the shorthand , contains information about the direction of the curve at position that we will use to calculate curvature.

At the beginning of this section we defined curvature, , as the rate at which the tangent is changing direction. We can now formalize this by differentiating with respect to arc length:

Where is the second derivative of the parameteric function :

When the tangent is placed into a cartesian plane its direction is related to the angle formed with the -axis (Figure 2). Thus the and components of the tangent vector can be expressed as:

Where:

And:

Thus, curvature can be expressed as the change in the angle formed between the tangent and the -axis:

This definition provides an intuitive unit of measurement for reporting curvature: degrees of rotation per unit arc length (Figure 2). For example, if arc length has been measured in millimeters, we would report its curvature as degrees per millimeter . Framed this way curvature is a measure of rotation per distance. In contrast to previous definitions, where curvature is an indivisible, single property of an entire shape, here, curvature is a property of every point along the curve. Under our point-wise definition, we can summarize the *total curvature* (Milnor, [1954](#ref-milnor_1954)) of a specimen as the of sum the individual curvature measurements made along the curve:

Units for *total curvature* are no longer expressed as because we are not measuring curvature at a single point. Instead we are summarizing all tangent rotations along the curve, expressed simply as .

   To account for size variation between specimens, we propose using *total adjusted curvature*, that is, total curvature divided by arc length:

Units for are expressed as . *Total adjusted curvature* also represents mean curvature of the curve.

#### A proposed protocol for measuring curvature

As illustrated in the methodology review, our current protocols for measuring flower-pollinator curvature lack a conceptual unity. There are two main advantages of the curvature definition described in Section 3. First, curvature becomes a local property of the tissue or organ under study. This means that shape information is gathered at every point along the curve and can be examined and compared to other points within or between specimens. This differs from previous methods that take curvature as a indivisible property of the entire specimen. Second, because the revised definition comes directly from the field of differential geometry, we benefit from established, well-defined concepts that make clear what is meant by ‘curvature’. When the definition of curvature is concordant between these research areas, future advances in geometry can be more readily incorporated into morphological studies.

   In order to apply the point-wise definition of curvature, a biological organ or tissue needs to be reduced to a continuous function. To do this, we propose a protocol as illustrated in Figure 3. First, a specimen is landmarked at several locations along the area of study. Second, a mathematical function is fitted to the landmarks, and finally, curvature is calculated point-wise along the curve. The long-term goal of this proposal is to integrate the analysis of curvature with existing morphometrics protocols. In the ‘proof-of-concept’ (Section 5) we use existing morphometric tools for landmarking and curve-fitting - these were previously developed in the field of ‘traditional morphometrics’ (e.g. Rohlf, [1990](#ref-rohlf_1990); MacLeod and Rose, [1993](#ref-macleod_1993); Terral et al., [2004](#ref-terral_2004)). As mentioned in the section *What is curvature?*, the field of plant physiology was an early adopter of the point-wise definition of curvature. In one case we found curvature (as defined above) computed from cubic functions fitted to cucumber seedlings that had been landmarked by hand (Cosgrove, [1990](#ref-cosgrove_1990)). Our protocol can be seen as a computerized version of this procedure. In another study, total curvature of *Anthurium* Schott (Araceae) spadices was computed from fitted B-spline curves (Pour et al., [2018](#ref-pour_2018)). However, because landmarks were not defined and the scripts are not publicly available, the reproducability of this protocol is low. Here, we propose to develop the analysis of curvature specifically within the R programming environment (R Core Team, [2017](#ref-R_2017)), where existing landmarking and curve-fitting procedures can be called, and where modern morphometrics is being most actively developed (e.g. within the open-source packages geomorph (Adams and Otárola-Castillo, [2013](#ref-adams_2013)) and Momocs (Bonhomme et al., [2014](#ref-bonhomme_2014))).

   In following section we calculate curvature from fitted-polynomials simply to illustrate the utility of a point-wise definition of curvature. Polynomial functions will not always be appropriate, and we encourage the development of algorithms that compute curvature from other curve-fitting strategies (reviewed in Rohlf, [1990](#ref-rohlf_1990)). Furthermore, there is potential for existing *geometric* morphometric (*sensu* Webster and Sheets, [2010](#ref-webster_2010)) algorithms to be modified to compute curvature. Within the field of *outline-based geometric morphometrics*, the tangent angle function, , has been used in Fourier Analysis to (very accurately) describe closed outlines of biological specimens (Zahn and Roskies, [1972](#ref-zahn_1972); Bookstein, [1978](#ref-bookstein_1978)). The tangent angle function, , describes the change in angle of a tangent vector as a function of distance traveled along the outline. This is equivalent to the definition of curvature, , described in Section 3. Therefore there is great opportunity for existing algorithms (e.g. Claude, [2008](#ref-claude_2008)) to parse curvature data as a part of an outline morphometrics analysis.

#### Proof of concept: A study of the development of curvature in *Epimedium*

*Study System*

We tested the utility of this curvature metric by studying floral development in *Epimedium* L. (Berberidaceae), a group of temperate, perennial herbs that inhabit montane ecosystems from North Africa to East Asia. *Epimedium* is perhaps best recognized by species having an elongated, curved nectar spur - a derived trait for pollination by bees (Stearn, [2002](#ref-stearn_2002)). Although widepread throughout *Epimedium*, the ecological function of nectar spur cuvature is largely unstudied. Early work comparing sympatric short- and long-spurred species found evidence for pollinator partioning in Japanese *Epimedium* ((Suzuki, [1984](#ref-suzuki_1984))): long-horned bees with short proboscides (*Eucerea nipponensis* Pérez) tend to visit *Epimedium trifoliolatobinatum* Koidz (spur length 10-15 mm), while bumblebees with longer proboscides ( *Bombus diversus* Smith) visit *Epimedium grandiflorum* C.Morren (spur length 10-20 mm. While these pollinators are nectar foraging, ([1984](#ref-suzuki_1984)) also found that pollen-collecting bees ( *Andrena* Fabricius and *Lassioglossum* Curtis) visit *Epimedium* indiscriminately, potentially contributing to hybridization. Although, both *E. trifoliolatobinatum* and *E. grandiflorum* exhibit strong floral curvature, the implications of curvature on pollinator partitoning have yet to be considered.

   In this study we examined the *Epimedium grandiflorum* complex [stearn\_2002, pp. 140-142] to determine whether floral morphology varied between the taxa *Epimedium grandiflorum* var. *koreanum* (Nakai) K.Suzuki (‘*E. koreanum*’), and *Epimedium grandiflorum* f. *violaceum* (C.Morren) Stearn (‘*E. violaceum*’). Because *E. grandiflorum sensu lato* encompasses several taxa that are not recognized as separate species, we examined floral morphology, including curvature, to determine the plausibility of assortative pollination mediated by flower shape.

   Flower size of *E. koreanum* and *E. violaceum* was measured daily from April 9 to May 2, 2019 at the UBC Botanical Garden (TableS2, Supplementary Methods 1). Size was defined as the distance between the apex of the two outer sepals lying on the major axis of the flower (aestivation is imbricate). Width was measured to the nearest 0.1 mm using an SPI Polymid Dial Caliper. By correlating changes in flower size to developmental landmarks (Figure S3), we were able to define 4 discrete size-stages in *E. koreanum* and *E. violaceum* (Table S3, Figure S4).

   To measure curvature, a set of *Epimedium* flowers at various stages of development (=58) were sampled haphazardly and preserved in 70% ethanol. Preserved flowers were later transferred to a glass slide and imaged in the dorsiventral view using a stereo microscope at 0.63x (Zeiss Stemi 508 with Axiocam 301). Specimens that did not fit within the field of view were imaged in halves and the images joined using the Stitching Plugin in the Fiji distribution of ImageJ2 (Preibisch et al., [2009](#ref-preibisch_2009); Rueden et al., [2017](#ref-rueden_2017)). Images were then processed using the protocol outlined in Section 4 (detailed in Supp Mat). We analysed how shape varied with developmental stage using the R package geomorph v.3.2.0 (Adams and Otárola-Castillo, [2013](#ref-adams_2013)). Curvature (as defined in Section 3) was calculated using the R package curvr v.0.0.1.

*Results and Discussion*

   At maturity, flower size and shape does not differ between taxa (Table SXXX, Figure S4). However, the flowers of *E. koreanum* take about 2 days longer to reach each of the developmental stages defined above (Table SXXX, Figure S5). At the earliest stage of development, shape differs between the two species (p=0.010, Z=3.21 units?); at maturity both species converge in shape (p=0.125, Z=1.23 units?). Morphometric analysis of developmental trajectories suggested that differences in shape might be attributed to nectar spur curvature (Figure 4).

   A subsequent analysis of curvature found that in early development, the nectar spurs of *E. koreanum* have on average 3.69 degrees/mm more curvature than *E. violaceum* (p=0.0042, *t*-ratio=5.4). In support of the trajectory analysis, there were no interspecific differences in curvature as the flowers reached maturity (Table SXXX, Figure S5).

   We interpret these patterns as an example of heterochrony leading to convergence in shape. In *E. koreanum* nectar spur curvature develops early, becoming less curved as the spurs emerge from the flower bud and elongate. In *E. violaceum*, young flowers have the same total mean curvature as mature flowers. As discussed in Section 1, it is possible that curvature develops in flower buds in response to a constraint for space. In the case of *E. koreanum* this early onset curvature is corrected as the nectar spur matures so that at maturity, there is no difference in shape between the two taxa. Divergence in floral development as observed here (“acceleration” sensu Rudall and Bateman, [2004](#ref-rudall_2004)) is a preadaptive trait that has the potential to generate floral diversity (reviewed in Rudall and Bateman, [2004](#ref-rudall_2004)). Although the taxa studied here are a part of the *E. grandiflorum* complex, differences in the development of curvature suggest that heterochrony might play a role in generating floral diversity within *Epimedium* at large.

*Conclusions*

   In this synthesis we discussed the ecological significance of curvature within the field of pollination ecology. In reviewing the methods used to measure curvature, we found that curvature is lacking a conceptual and methodological unity. By drawing from the geometry literature we aimed to clarify the definition of curvature within the contexts most commonly used in pollination ecology: the curvature of floral tubes or pollinator mouthparts as viewed from the dorsiventral plane. We demonstrated the utility of this revised metric by analysing the development of curved nectar spurs in *Epimedium*. An explicit analysis of curvature can complement morphometric analyses where curvature is identified as a principle component correlated with changes in shape.

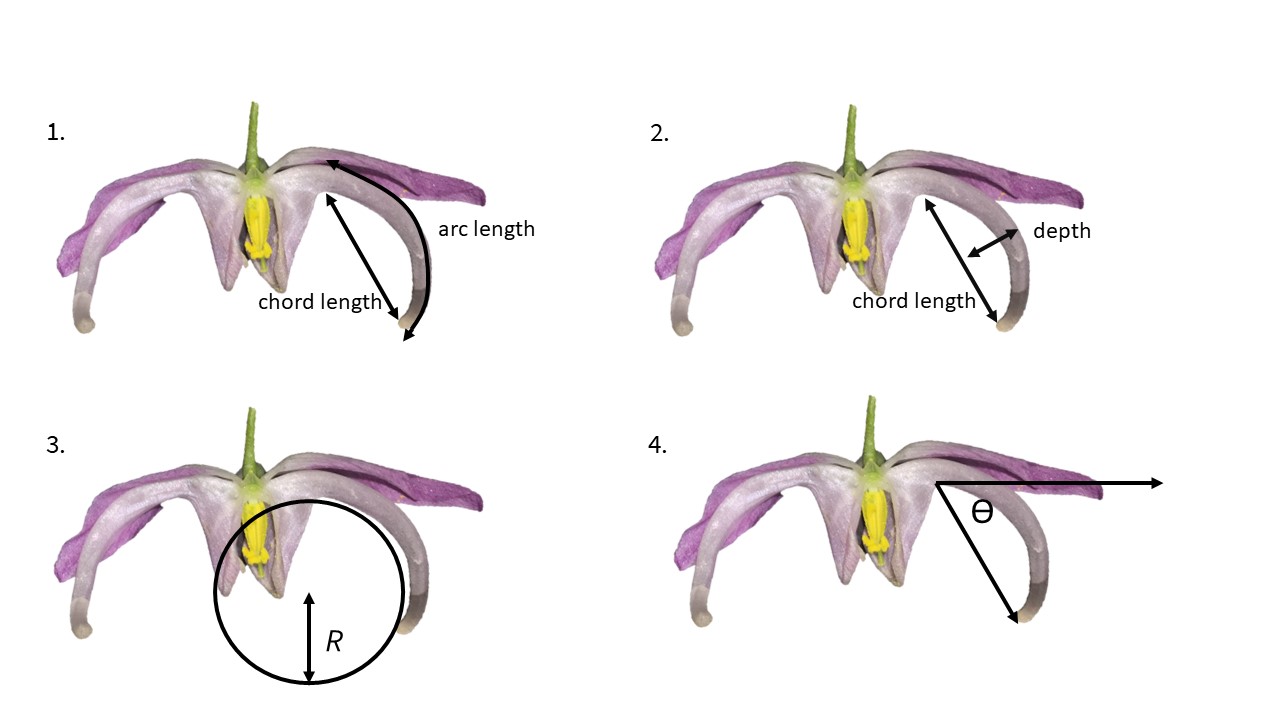


Figure 1. Overview of most commonly used curvature metrics within pollination ecology. 1. arc:chord ratio. 2. mandibular index 3. inverse radius. 4. angle of deflection

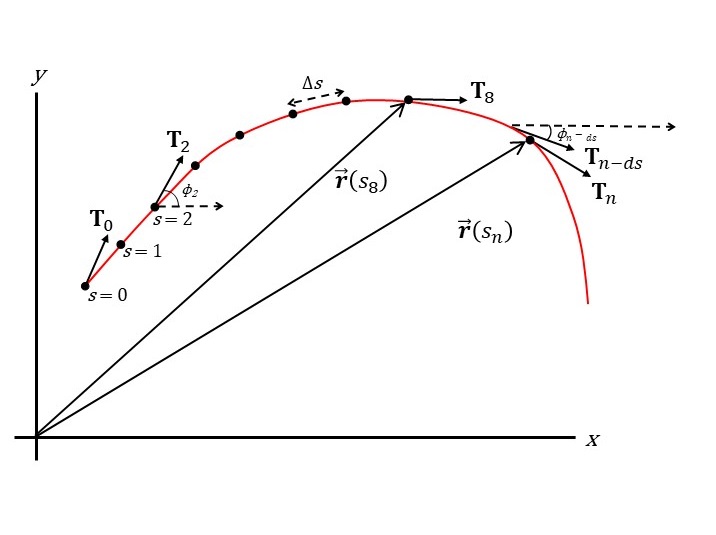
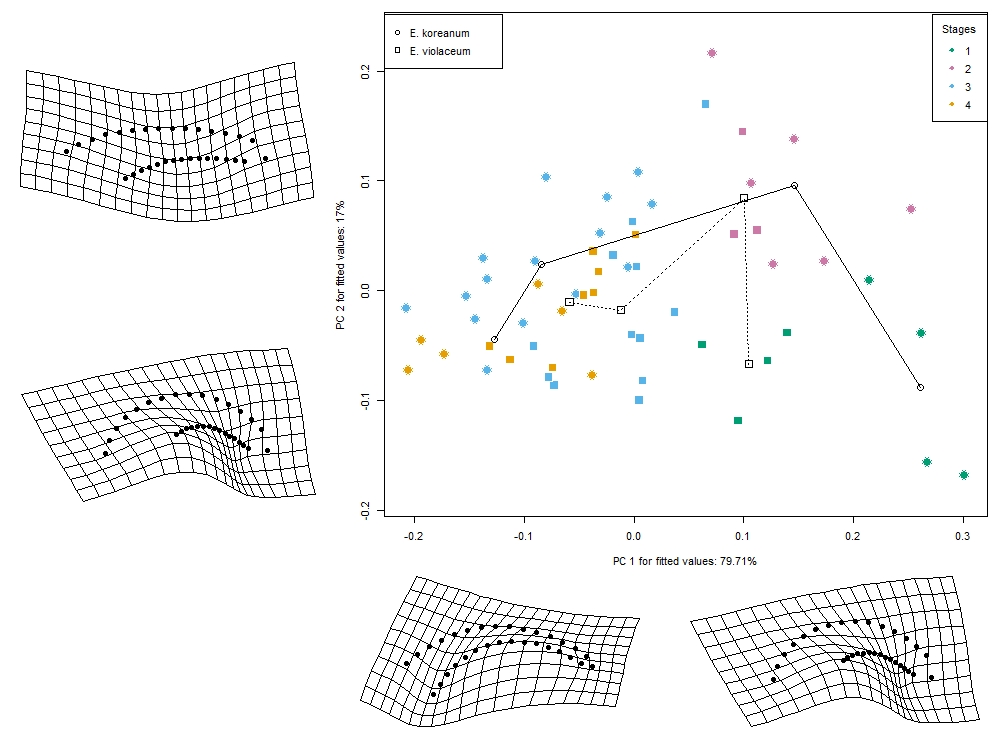


Figure 2. A curve parameterized by arc length, . When , the vector points to the location on the curve . , , and are the tangents ( ) at , , and , respectively. Curvature at is defined in Section 3.



Figure 3: Proposed protocol for measuring curvature. 1. A specimen (in this case *Epimedium violaceum*) is landmarked, semi-landmarked and assigned *xy* coordinates within a Cartesian plane. 2. The *xy* coordinates are rotated so that a single-valued function can be fitted to the landmarks. 3. The tangent vector is calculated at an arbitrarily large number of increments, , along the curve. 4. Curvature is calculated as the rate of change of the tangent vectors point-wise along the curve. Total curvature is calculated by the methods outlined in Section 3.



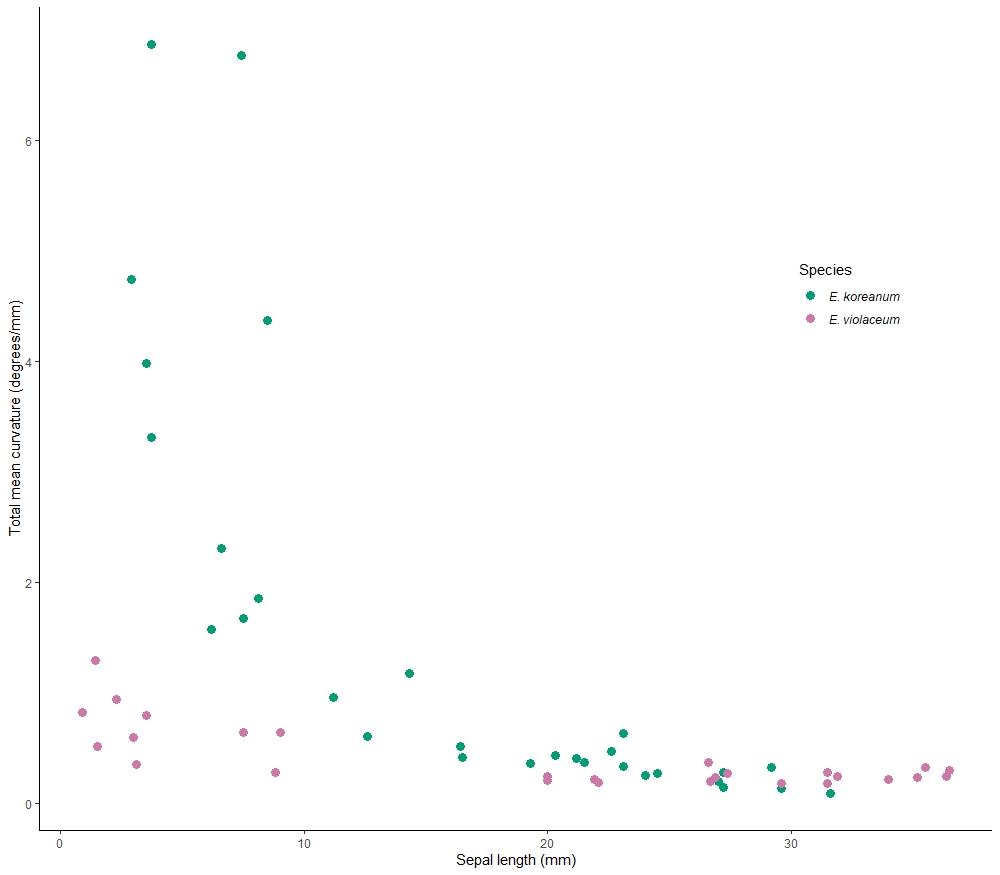


Figure 5: size vs curvature

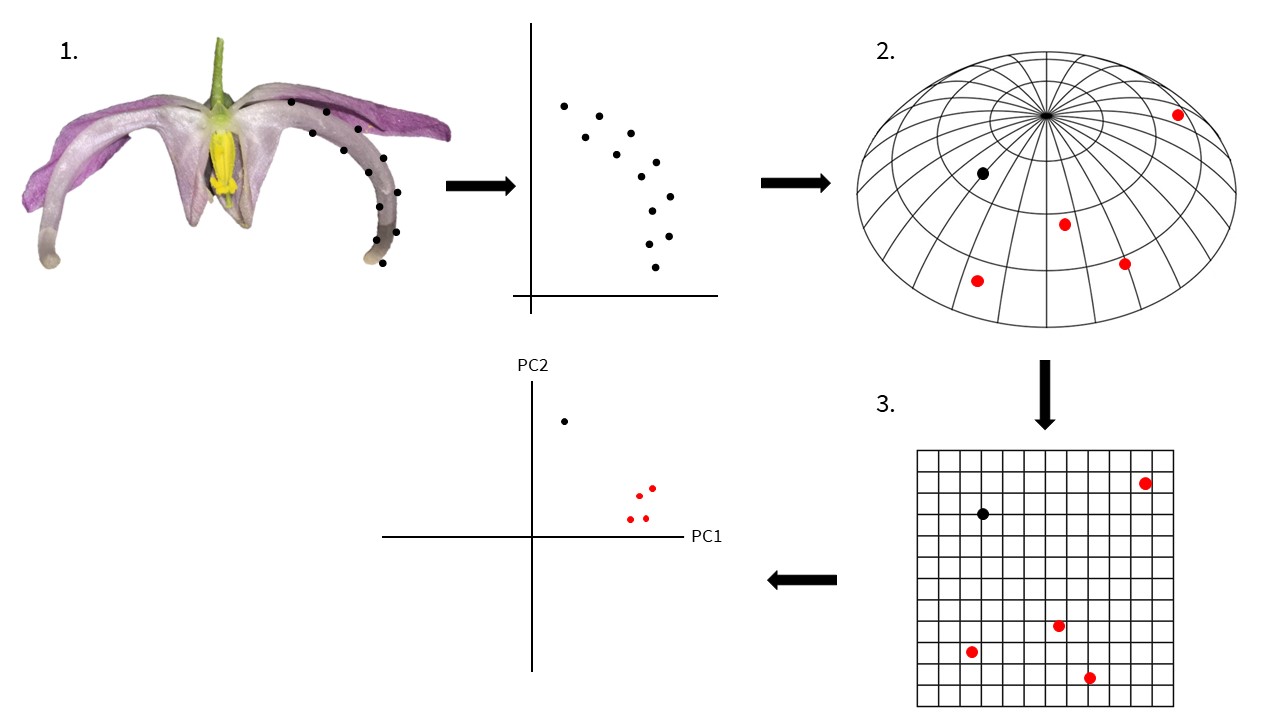


Figure S1. Demonstration that the angle of deflection and inverse radius methods are interchangeable

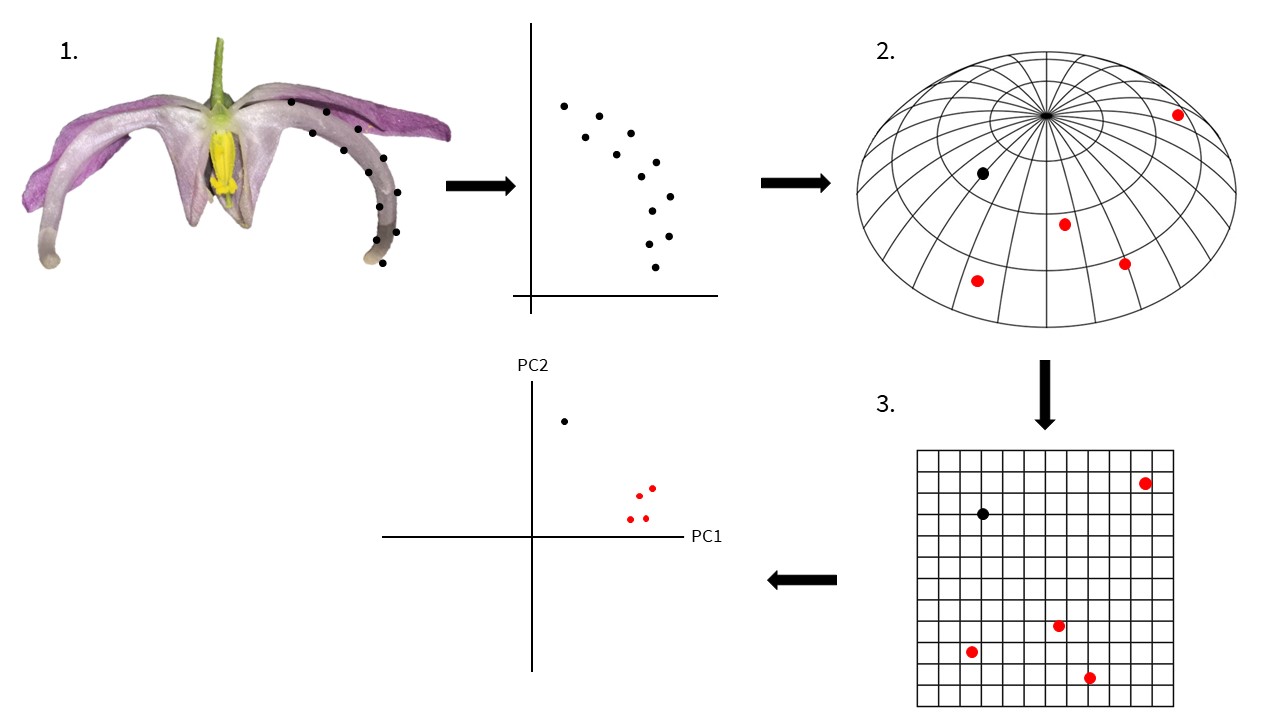


Figure S2. Overview of a geometric morphometrics protocol. 1. Landmarks and semi-landmarks are assigned to a specimen. Each landmark is assigned an xy coordinate. 2. For each specimen a configuration of landmarks exists as a single point in a non-Euclidian shape space (abstracted here as a sphere segment). Red points represent landmark configurations from other specimens. 3. Shape data is projected onto a Euclidian plane – a tangent space approximation. This allows statistical analyses of shape variation (e.g. principal components analysis).



Figure S3. Landmarks (red) and semi-landmarks (white) used to compare curvature between *E. koreanum* (left) and *E. violaceum* (right). Petals sampled at anthesis.

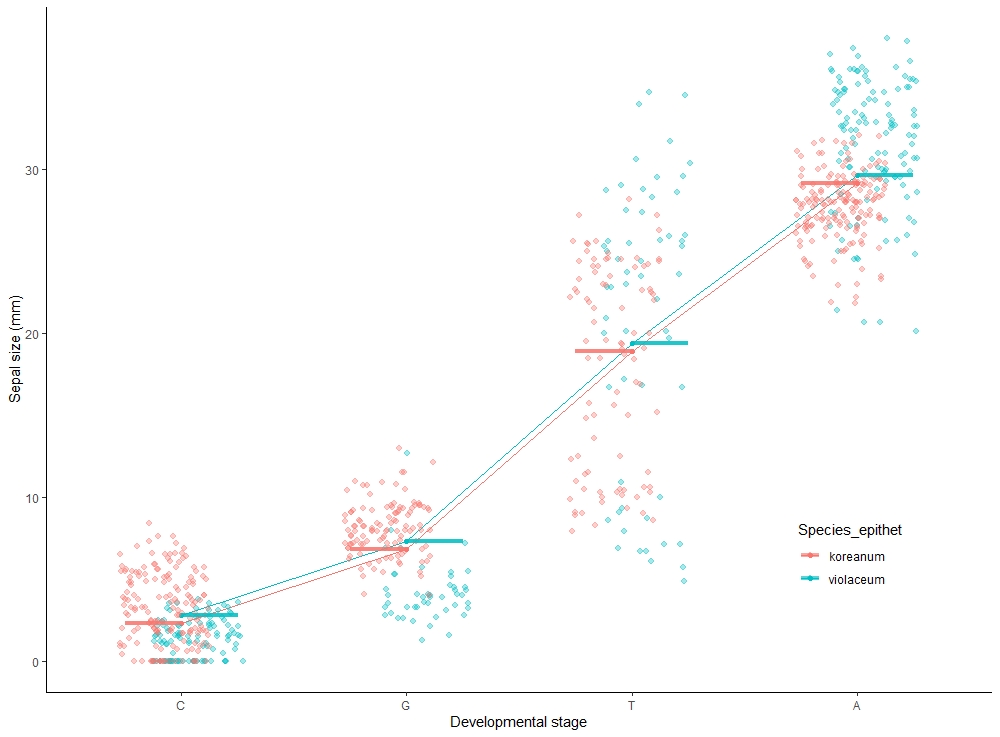


Figure S4: Comparison of developmental stages and size in *Epimedium*. Tukey’s HSD: p<0.01 for all within-species comparisons.

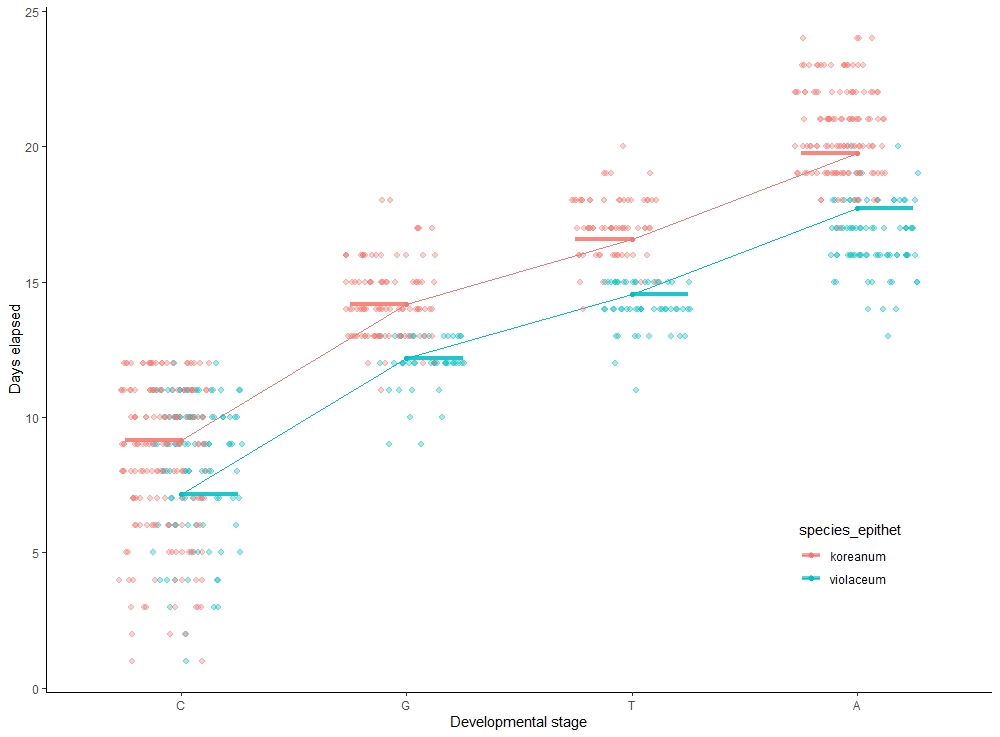


Figure S5: Comparison of timing of developmental stages in *Epimedium*. Size is in mm. Tukey’s HSD: p<0.01 for all within-species comparisons

Table 1: Summary of literature reviewed for the role of curvature in plant-pollinator systems.

|  |  |  |
| --- | --- | --- |
| Citation | System | Stated or Inferred Method |
| Feinsinger and Colwell ([1978](#ref-feinsinger_1978)) | Community organization among neotropical nectar-feeding birds | arc:chord ratio |
| Snow and Snow ([1972](#ref-snow_1972)) | Feeding niches of hummingbirds in a Trinidad valley | qualitative |
| Stiles ([1975](#ref-stiles_1975)) | Corolla morphology of *Heliconia* (Zingerberales) and bill morphology of nine hummingbird species at La Selva, Costa Rica. | qualitative |
| Gill and Wolf ([1978](#ref-gill_1978)) | Sunbird bill diversity and abilities to extract nectar from Kenyan *Leonotis nepetifolia* (Lamiaceae). | mandibular index |
| Carothers ([1982](#ref-carothers_1982)) | Effects of trophic morphology and behavior on foraging rates of three Hawaiian honeycreeper | angle of deflection |
| Grant and Grant ([1983](#ref-grant_1983)) | Hawkmoth pollination of *Mirabilis longiflora* (Nyctaginaceae) | qualitative |
| Paton and Collins ([1989](#ref-paton_1989)) | Correlates (Geography, Age, Sex, Tongue structure, foraging mode) of bill morphology on nectar extraction 198 hummers (and other birds). | mandibular index |
| Smith et al. ([1995](#ref-smith_1995)) | Evolutionary Consequences of Extinctions in Populations of a Hawaiian Honeycreeper | inverse radius |
| Stiles ([1995](#ref-stiles_1995)) | Effects of bill morphology on insect foraging strategy by 11 species of hummingbirds at La Selva, Costa Rica. | arc:chord ratio |
| Mclntyre and Browne ([1996](#ref-mcintyre_1996)) | Phototropism in Helianthus and effects on cotyledon curvature | angle of deflection |
| Cotton ([1998](#ref-cotton_1998)) | Survey and description of 16 hummingbird species occurring at Amacayacu National Park, Colombia. | qualitative |
| Temeles et al. ([2000](#ref-temeles_2000)) | Sexual dimorphism of bill shape in Purple-throated caribs (*Eulampis jugularis*), pollinatiors of *Heliconia* at Quilesse Reserve, Saint Lucia. | angle of deflection, inverse radius |
| Borgella Jr et al. ([2001](#ref-borgella_2001)) | Effects of bill morphology (21 hummingbird spp.) on pollen loads (35 plant spp.) at Coto Brus, Costa Rica. | arc:chord ratio |
| Temeles and Kress ([2003](#ref-temeles_2003)) | Floral curvature in *Heliconia* pollinated by purple-throated caribs (*Eulampis jugularis*) | angle of deflection |
| Travers et al. ([2003](#ref-travers_2003)) | Nectar spurs of Impatiens spp. and Ruby-throated hummingbird (Archilochus colubris) at Franklin County, Massachusetts. | angle of deflection |
| Temeles et al. ([2005](#ref-temeles_2005)) | Sexual dimorphism of bill shape in Purple-throated caribs (Eulampis jugularis), pollinatiors of Heliconia at Quilesse Reserve, Saint Lucia. | angle of deflection, inverse radius |
| Collins ([2008](#ref-collins_2008)) | Foraging efficiency from artificial and natural (15 spp.) flowers by 4 species of hummingbirds at Monteverde, Costa Rica | mandibular index |
| Stiles ([2008](#ref-stiles_2008)) | Correlations of bill morphology to the elevational distributions of 150 spp. of hummingbirds in the Andes. | arc:chord ratio |
| Young ([2008](#ref-young_2008)) | Selection on spur shape in *Impatiens capensis* (Balsaminaceae) | angle of deflection |
| Martén-Rodrı́guez et al. ([2009](#ref-marten_2009)) | Testing the pollination syndrome hypothesis in Antillean Gesneriaceae. | angle of deflection |
| Temeles et al. ([2009](#ref-temeles_2009)) | Effects of natural (*Heliconia*) and artificial flower morphologies on foraging performance of purple-throated caribs (*Eulampis jugularis*) at Saint Lucia. | angle of deflection, inverse radius |
| Luo and Li ([2010](#ref-luo_2010)) | Effects of light and low temperature on the reciprocal style curvature of flexistylous *Alpinia* (Zingiberaceae) | angle of deflection |
| Temeles et al. ([2010](#ref-temeles_2010)) | Sexual dimorphism of bill shape in 21 species of Central and South American hummingbirds. | angle of deflection, inverse radius |
| Berns and Adams ([2010](#ref-berns_2010)) | Sexual dimorphism of bill shape in black-chinned hummingbird (*Archilochus alexandri*) and ruby-throated hummingbird (*Archilochus colubris*). | geometric morphometrics |
| Berns and Adams ([2013](#ref-berns_2013)) | Sexual dimorphism of bill shape in 219 hummingbird spp. | geometric morphometrics |
| Wang et al. ([2013](#ref-wang_2013)) | Pollinators and nectar robbers cause directional selection for large spur circle in *Impatiens oxyanthera* (Balsaminaceae) | angle of deflection |
| Maglianesi et al. ([2014](#ref-maglianesi_2014)) | Trait matching and resource use in a plant-hummingbird network, La Selva, Costa Rica. | angle of deflection |
| Rico-Guevara and Araya-Salas ([2014](#ref-rico_2014)) | Bills as weapons in lekking *Phaethornis longirostris* at La Selva, Costa Rica. | arc:chord ratio |
| Alexandre et al. ([2015](#ref-alexandre_2015)) | QTL analysis comparing hummingbird pollinated and generalist *Rhytidophyllum* flowers (Gesneriaceae). | angle of deflection |
| Maglianesi et al. ([2015b](#ref-maglianesi_2015_a)) | Differential preferences of artificial and natural (65 spp.) flower populations visited by 3 species of hummingbird in Braulio Carrillo National Park, Costa Rica. | angle of deflection |
| Maglianesi et al. ([2015a](#ref-maglianesi_2015_b)) | Plant-pollinator specialization along an elevational gradient at Braulio Carrillo National Park, Costa Rica. 21 hummingbird spp. and 208 plant species examined. | angle of deflection |
| Rocha et al. ([2015](#ref-rocha_2015)) | Auxin and physical constraint exerted by the perianth promote androgynophore bending in *Passiflora mucronata* (Passifloraceae) | arc:chord ratio |
| Miller et al. ([2017](#ref-miller_2017)) | Ecological divergence among closely related, morphologically similar honeyeaters co-occurring in arid Australian environments | arc:chord ratio |
| Lagomarsino et al. ([2017](#ref-lagomarsino_2017)) | Evolution of pollination syndromes in Andean Campanulaceae. | arc:chord ratio |
| Boehm ([2018](#ref-boehm_2018)) | Review of nectar robbing in *Centropogon* (Campanulaceae) | qualitative |
| Hadley et al. ([2018](#ref-hadley_2018)) | Effects of forest fragmentation on hummingbird bill morphologies (19 spp.) representative of specialization. Coto Brus, Costa Rica. | arc:chord ratio |
| Joly et al. ([2018](#ref-joly_2018)) | Analysis of polliation syndromes in Antillean Gesneriaceae. | geometric morphometrics |
| Partida-Lara et al. ([2018](#ref-partida_2018)) | Spatio-temporal structure of the taxonomic and functional diversity of hummingbirds at the biosphere reserve El Triunfo, Chiapas, Mexico | inverse radius |
| Dellinger et al. ([2019](#ref-dellinger_2019)) | Floral trait changes correlated with the repeated shifts away from buzz pollination in the Melastomataceae. | qualitative |
| Sonne et al. ([2019](#ref-sonne_2019)) | Distribution of morphological specialization along an elevational gradientin Ecuador. | arc:chord ratio |

Table S1: Additional literature reviewed for the role of curvature in plant-pollinator systems.

|  |  |  |
| --- | --- | --- |
| Citation | System | Stated or Inferred Method |
| Baldwin et al. ([1931](#ref-baldwin_1931)) | Measurements of birds | inverse radius |
| Hamilton ([1975](#ref-hamilton_1975)) | Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae) | inverse radius |
| Buttrose et al. ([1977](#ref-buttrose_1977)) | Significance of curvature of style branches in *Hibiscus trionum* (Malvaceae) for pollination | qualitative |
| Mountainspring ([1987](#ref-mountainspring_1987)) | sexual dimorphism and foraging preferences of the Hawaiian honeycreeper (*Pseudonestor xanthophrys*) | mandibular index |
| Muller ([1995](#ref-muller_1995)) | curved bristles on the proboscis on European bees for the extraction of pollen. | qualitative |
| Manning and Goldblatt ([1997](#ref-manning_1997)) | Tangle-veined fly pollination of South African Iridaceace, Geraniaceae, Orchidaceae | qualitative |
| Ortiz et al. ([2000](#ref-ortiz_2000)) | Pollination and breeding system of *Putoria calabrica* (Rubiaceae), a Mediterranean dwarf shrub | qualitative |
| Lindqvist et al. ([2003](#ref-lindqvist_2003)) | Cladogenesis and reticulation in the Hawaiian endemic mints (Lamiaceae) | qualitative |
| Ruan et al. ([2008](#ref-ruan_2008)) | The impact of pollen tube growth on stigma lobe curvature in *Kosteletzkya virginica* (Malvaceae) | qualitative |
| Kawabata et al. ([2009](#ref-kawabata_2009)) | Quantitative analysis of corolla shapes and petal contours in single-flower cultivars of *Lisianthus* (Gentianaceae) | fourier analysis |
| Dalayap et al. ([2011](#ref-dalayap_2011)) | Petal, sepal, and labellum shapes in Mokara orchids (Orchidaceae) | geometric morphometrics |
| Nii and Kawabata ([2011](#ref-nii_2011)) | Assessment of the association between the three-dimensional shape of the corolla and two-dimensional shapes of petals using Fourier descriptors and principal component analysis in *Eustoma grandiflorum* (Gentianaceae) | fourier analysis |
| Campos et al. ([2015](#ref-campos_2015)) | Generating 3D printed flowers to test efficacy of moth pollination | curve decay parameter |
| Berger et al. ([2017](#ref-berger_2017)) | Quantifying morphological modifications to floral form in gene knockdowns in *Fedia graciliflora* (Caprifoliaceae) | geometric morphometrics |
| Pour et al. ([2018](#ref-pour_2018)) | Curvature-based pattern recognition for cultivar classification of *Anthurium* (Araceae) flowers | point-wise curvature |
| Song et al. ([2018](#ref-song_2018)) | Quantitative classification of the morphological traits of ray florets in large-flowered *Chrysanthemum* (Asteraceae) | angle of deflection |
| Peng et al. ([2019](#ref-peng_2019)) | Morphospace exploration reveals divergent fitness optima between plants and pollinators | curve decay parameter |

Table S2: Sample sizes.

|  |  |  |  |
| --- | --- | --- | --- |
| Species | n (Individuals) | n (total panicles) | n (total flowers) |
| E. koreanum | 2 | 11 | 50 |
| E. violaceum | 2 | 3 | 33 |

Table S3: Stages of *Epimedium* flower development.

|  |  |  |
| --- | --- | --- |
| Citation | System | Stated or Inferred Method |
| Feinsinger and Colwell ([1978](#ref-feinsinger_1978)) | Community organization among neotropical nectar-feeding birds | arc:chord ratio |
| Snow and Snow ([1972](#ref-snow_1972)) | Feeding niches of hummingbirds in a Trinidad valley | qualitative |
| Stiles ([1975](#ref-stiles_1975)) | Corolla morphology of *Heliconia* (Zingerberales) and bill morphology of nine hummingbird species at La Selva, Costa Rica. | qualitative |
| Gill and Wolf ([1978](#ref-gill_1978)) | Sunbird bill diversity and abilities to extract nectar from Kenyan *Leonotis nepetifolia* (Lamiaceae). | mandibular index |
| Carothers ([1982](#ref-carothers_1982)) | Effects of trophic morphology and behavior on foraging rates of three Hawaiian honeycreeper | angle of deflection |
| Grant and Grant ([1983](#ref-grant_1983)) | Hawkmoth pollination of *Mirabilis longiflora* (Nyctaginaceae) | qualitative |
| Paton and Collins ([1989](#ref-paton_1989)) | Correlates (Geography, Age, Sex, Tongue structure, foraging mode) of bill morphology on nectar extraction 198 hummers (and other birds). | mandibular index |
| Smith et al. ([1995](#ref-smith_1995)) | Evolutionary Consequences of Extinctions in Populations of a Hawaiian Honeycreeper | inverse radius |
| Stiles ([1995](#ref-stiles_1995)) | Effects of bill morphology on insect foraging strategy by 11 species of hummingbirds at La Selva, Costa Rica. | arc:chord ratio |
| Mclntyre and Browne ([1996](#ref-mcintyre_1996)) | Phototropism in Helianthus and effects on cotyledon curvature | angle of deflection |
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| Young ([2008](#ref-young_2008)) | Selection on spur shape in *Impatiens capensis* (Balsaminaceae) | angle of deflection |
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| Maglianesi et al. ([2014](#ref-maglianesi_2014)) | Trait matching and resource use in a plant-hummingbird network, La Selva, Costa Rica. | angle of deflection |
| Rico-Guevara and Araya-Salas ([2014](#ref-rico_2014)) | Bills as weapons in lekking *Phaethornis longirostris* at La Selva, Costa Rica. | arc:chord ratio |
| Alexandre et al. ([2015](#ref-alexandre_2015)) | QTL analysis comparing hummingbird pollinated and generalist *Rhytidophyllum* flowers (Gesneriaceae). | angle of deflection |
| Maglianesi et al. ([2015b](#ref-maglianesi_2015_a)) | Differential preferences of artificial and natural (65 spp.) flower populations visited by 3 species of hummingbird in Braulio Carrillo National Park, Costa Rica. | angle of deflection |
| Maglianesi et al. ([2015a](#ref-maglianesi_2015_b)) | Plant-pollinator specialization along an elevational gradient at Braulio Carrillo National Park, Costa Rica. 21 hummingbird spp. and 208 plant species examined. | angle of deflection |
| Rocha et al. ([2015](#ref-rocha_2015)) | Auxin and physical constraint exerted by the perianth promote androgynophore bending in *Passiflora mucronata* (Passifloraceae) | arc:chord ratio |
| Miller et al. ([2017](#ref-miller_2017)) | Ecological divergence among closely related, morphologically similar honeyeaters co-occurring in arid Australian environments | arc:chord ratio |
| Lagomarsino et al. ([2017](#ref-lagomarsino_2017)) | Evolution of pollination syndromes in Andean Campanulaceae. | arc:chord ratio |
| Boehm ([2018](#ref-boehm_2018)) | Review of nectar robbing in *Centropogon* (Campanulaceae) | qualitative |
| Hadley et al. ([2018](#ref-hadley_2018)) | Effects of forest fragmentation on hummingbird bill morphologies (19 spp.) representative of specialization. Coto Brus, Costa Rica. | arc:chord ratio |
| Joly et al. ([2018](#ref-joly_2018)) | Analysis of polliation syndromes in Antillean Gesneriaceae. | geometric morphometrics |
| Partida-Lara et al. ([2018](#ref-partida_2018)) | Spatio-temporal structure of the taxonomic and functional diversity of hummingbirds at the biosphere reserve El Triunfo, Chiapas, Mexico | inverse radius |
| Dellinger et al. ([2019](#ref-dellinger_2019)) | Floral trait changes correlated with the repeated shifts away from buzz pollination in the Melastomataceae. | qualitative |
| Sonne et al. ([2019](#ref-sonne_2019)) | Distribution of morphological specialization along an elevational gradientin Ecuador. | arc:chord ratio |

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