**Erol Akçay (Co-Editor)**  
  
1. [I] will emphasize that especially the description of the geometric measures you are proposing. As Reviewer 2 notes, there are some points that would be good to clarify in that regard. **We have attempted to address these points in our response to Comment #2, Reviewer #2 (page 10 of this document).**

2. I should also emphasize that making your code available for the revision will be important.

**We have included a Dryad repository with an R Studio project that allows the reproduction of our curvature estimates from the Epimedium dataset:**

**Link for reviewers:** [**https://datadryad.org/stash/share/H6-pYak3rTA2ohDrmZSl7cf4zYO9UZ-oqNVEKXdWIug**](https://datadryad.org/stash/share/H6-pYak3rTA2ohDrmZSl7cf4zYO9UZ-oqNVEKXdWIug)

3. My own reading also left me wondering what specifically we have learned from the example analysis of Epidemic development. Partly this is again because I am not sure how the floral shape is defined (does it incorporate the curvature or not? Seems like it does, but what else does it include — weird to spend this much time explicitly on a measure only for it to disappear into a PCA in the results.). **We have attempted to (succinctly) define ‘shape’ at lines 210-211 and 273-275. However, a more detailed discussion by Bookstein (1991) is cited at line 252. Shape (sensu Bookstein 1991) implicitly contains curvature information, and much more (e.g. chord length, arc length), but is not the focus of typical GM analyses (lines 286-290).**

4. But also the overall biological message. I understand that this is mainly a methodological paper (which is fine) and a principled unification of curvature measurement is worthy in itself, but I think it would make the paper stronger if you can demonstrate that this method gets at something other methods cannot (or do not as well). **Agreed. We have more explicitly stated the overall biological message at lines 448-453, and discussed this message in the context of the *Epimedium* study at lines 513-535.**

5. Please be careful in your revision to add as little as possible to the length of the text, and any ability to condense a bit here and there would be appreciated. **We have been careful to add in the reviewer’s suggestions while also paring down other parts of the manuscript. The revised main text has 292 more words than our original submission, with a total of 6091 words.**

**Marjorie Weber (Associate Editor)**  
  
1. The caveats of the new approach for measuring curvature presented by the authors needs to be clearly articulated. As reviewer 1 points out, these caveats are critical for readers to be able to interpret the pros and cons of this method and choose among the reviewed approaches. In most cases these can be addressed simply by stating the caveats more clearly in the paper. However, I agree with reviewer 1 that including a correlation between the geometric measure of curvature and length across the 57 measured flowers would allow for a nice assessment of the confounding nature of length in their proposed approach.

**We have added a brief mention of caveats and potential sources of error in the main text (lines 215-218 and 392-396). However, because the caveats are numerous, and vary with each study system, we have pointed the reader to two recent papers which address this issue at length and in detail (line 394).**

**We agree that a shortfall of the older methods is a lack of consideration of allometric effects, which includes correlation of chord length and arc length with total curvature. We have included a brief discussion of the allometry problem at lines 243-248. The issue of allometry for the proposed method is discussed at lines 358-367. However, these auto-correlations are not mathematical, but biological/developmental and will need to be addressed differently for each study system. More details on this point are given in our response to Comment #2b from Reviewer #1 (below).**

2. I also agree with reviewer 2’s important points, including that adding more details to the description of the point method into the main text, and making R scripts available, will be essential to allow for a more transparent evaluation of the methods and results, and to achieve the stated goal of making the point-wise approach easily accessed and used by other biologists interested in curvature. **Agreed. We have expanded on the methodological and R script details in the main text (starting at line 436), including specific package names, functions, and citations for readers to find these software. We have also included a Dryad repository with an R Studio project that allows the reproduction of our curvature estimates from the *Epimedium* dataset:**

**Link for reviewers:** <https://datadryad.org/stash/share/H6-pYak3rTA2ohDrmZSl7cf4zYO9UZ-oqNVEKXdWIug>

**Reviewer #1:**   
  
**Comment #1:** The authors limited their search of the literature on studies of curvature to pollination systems. Unfortunately, such a limited search can miss highly relevant papers such as this paper by R. Townsend Peterson:  
  
Peterson, RT (1993) Adaptive geographical variation in bill shape of scrub jays (Apelocoma coerulescens). American Naturalist 142(3): 508-527.  
  
Peterson uses methods to characterize bill curvature of jays that are quite similar to the authors' and bases his analyses on Bookstein's earlier papers. I think it is probably worth acknowledging the paper given that it was published in American Naturalist and that researchers on birds will likely know about it. Peterson's focus was on jays and not curvature measurements per se and the authors do a much better job of discussing the latter. I'll leave it to them to decide in how much detail to discuss this paper.

**> We appreciate the suggestion and have cited this paper in the context of applying the tangent angle function and fitting curves to landmarked specimens (lines 373-375).**

**However, Peterson (1993) uses tangent angles (essentially point curvature) to fit polynomials to the resultant tangent angle function, *not* to compare differences in total curvature (*K*)as we have defined it in this manuscript. In Peterson (1993), the parameters (A,B,C) from the polynomial are analysed on the basis of describing the curvature properties of the polynomial. We do not disagree with this approach, but it is fundamentally different from what we are proposing. For example, the y-axis in Figure 3 (Peterson 1993) could read “point-wise curvature (rad/mm)”, but in fact, measuring total curvature (*Ktot*) was not the goal of Peterson (1993) and it is not mentioned except in the methods for fitting polynomials.**

**Our literature search was limited to pollination ecology, which we believe to be appropriate given the significant influence that this field has on evolutionary ecology. Undoubtedly some related fields will have adopted more sophisticated morphometrics practices than others, but the goal of this paper is to address pollination ecology specifically, and fully accounting for the numerous related fields (e.g. plant physiology, passerine feeding ecology, taxonomy) would lengthen the manuscript considerably.**

**Comment #2** My next series of comments deal with a frank discussion of the pros and cons of the different methodologies for measuring curvature, which needs to be expanded:  
  
2a) First, one of the biggest drawbacks to the arc:chord method, the mandibular index, and the inverse radius method for measuring curvature is that these methods often produce measurements of curvature that are highly correlated with measurements of length (such as chord). These correlations present a problem in selection analyses (especially selection gradients) because the correlations between length and curvature can be so strong that their independent effects on fitness (survival or reproductive success) cannot be distinguished. Put bluntly, what is the point of measuring curvature if you cannot determine whether it or length is the actual target of selection?

**> We agree that a shortfall of the older methods is a lack of consideration of allometric effects, which includes correlation of chord length and arc length with total curvature. We have included a brief discussion of the allometry problem at lines 243-248. The issue of allometry for the proposed method is discussed at lines 358-367.**

2b) With comment (2a) in mind, it would be nice to assess whether the geometric morphometric method introduced here produces a measurement of curvature that is independent of length, where length would be the chord extending from the starting point to the end point in Fig. 3. The authors measured 57 flowers so they have the data to do so. Maybe correlations between curvature measurements and length are an inherent property of their geometry and there is nothing we can do about it.

**> We appreciate the comment, and note that there are two problems at hand:**

**1) This issue of whether total curvature (*Ktot*) is mathematically correlated with chord length, arc length, or other size metrics, and**

**2) Whether there are biological/developmental reasons why curvature might be constrained by size/arc length/chord length, etc.**

**To address the first issue: chord length and total curvature (*K*) are mathematically decoupled. The trajectory of the curve between the start and end coordinates is what determines *Ktot*. The Euclidean distance between the start and end coordinates (i.e. the chord) does not contain any information about curvature, and thus cannot influence *Ktot*, except that it defines the bounds of the computation. For example, if one specimen is fitted with a half unit circle (*r* = 1) and another larger specimen is fitted with a half circle with *r* = 2. In the smaller specimen, *K* = 180 deg, and chord = 2\**r* = 2. In the larger specimen, *K* is also 180 deg, but the chord is 4. A similar example is also given at lines 359-361.**

**At the same time, there could be a developmental/biological reason why total curvature and chord length, arc length, or other size measures are correlated. In the *Epimedium* study, arc length and curvature are somewhat negatively correlated (*p* = 0.049, *t* = -2.016,ηp2 = 0.07, see: ”8\_review.R” in the Dryad repository). This is possibly due to a developmental constraint on curvature, e.g. longer nectar spurs are less curved because curvature might develop early in development and straighten somewhat as the flower reaches anthesis. However, we emphasize that these measures are not correlated mathematically to total curvature. To demonstrate this, we generated 1000 random open curves bounded by x{0, 200} and y{0,20} and computed total curvature, arc length, and chord length in the same manner as with the *Epimedium* samples (see: ”8\_review.R” for code). For these 1000 curves, arc length varies independently of total curvature (*p* = 0.957, *t*998= 0.054, R2 = -0.0009), as does chord length (*p* = 0.836, *t*998= -0.207, R2 = -0.0009).**

**However, it is beyond the scope of this manuscript to discuss the numerous allometric scenarios that individual studies and organisms might present. Instead, we have laid out a conceptual framework to deal with allometry that can be applied to a wide range of study systems (lines 361-367); each unique study will need to adjust this framework to match their research question accordingly.**

2c) On lines 185-187, the authors discuss the benefits of the five earlier methods, particularly their portability and accessibility. I think the most important benefit is that they can be performed in inclement weather such as rain.

**> Agreed and included at lines 215-217.**   
  
2d) Although the authors discuss the benefits of their methodology based on geometric morphometrics for obtaining a more precise measurement of curvature, the do not address the limitations of this method. The most serious limitation is that to employ the method with accuracy, flowers and bills would have to be photographed at precisely the same angle. They took their photographs and measurements under a microscope. Their methodology has much less utility in field studies: high winds or rain may make photographs impossible to take. Moreover, for studies of selection on floral traits, the labor involved in employing their method may be impractical: a researcher may measure 5-10 flowers from 100 or more plants, replicated across multiple populations. I think it would help to be candid, here.

**> We agree that we need to be clear about what equipment/conditions are needed to use the proposed method, especially in the field. We have briefly included some practical advice related to this, but ultimately point the reader to Fruciano (2016) and Savriama (2018) who have dedicated entire manuscripts to best practices in GM. The former discusses at length the numerous sources of error in GM protocols, and ultimately it is up to the researcher to decide how to implement their data collection protocols to mitigate these errors.**

**We also agree that the need for standardized photos will limit the versatility of this method, however, this limitation is inherent to any photo-based method. Thus, the only weather-proof methods available are the ‘older methods’, and their own limitations need to be weighed with consideration of the research question.**

**Comment #3:** line 83: delete the word "by".

**> We believe the sentence makes sense as is: “As predicted by Stiles (2004), Maglianesi (2015a) and Sonne (2019) found plant-hummingbird curvature to be more represented across species in the lowlands of the Neotropics compared to higher elevations.” (now line 111).**   
  
**Comment #4**: lines 101-106: some hummingbird species, such as the swordbill, Ensifera ensifera, have bills that are curved upwards rather than downwards. Like passerines which use their decurved bills to pull flowers down to them, swordbills visit pendant flowers from below and pull the up.

**> Thank you for bringing this to our attention. We have included a mention of this at lines 99-106.**

**Comment #5:** line 110: it's inaccurate to say that bill curvature only occurs in the Phaethornithinae. Many trochilids also have curved bills: Campylopterus species, Lafresnaya, Ensifera, Opisthoprora euryptera, Calothorax lucifer, etc.

**Agreed. Although, the genera listed above do have curved billed species, they are spread throughout multiple subfamilies (Stiles 2008), whereas the Hermits are a single subfamily with >30 curved billed species. We have adjusted the wording to reflect this fact (lines 137-139).**

**Comment #6:** Perhaps the most important point to make is that authors need to use the correct terminology for their measurements. The authors' method is assessing shape. The inverse radius method is assessing curvature of a circle. The angle of declension is assessing exactly what its name implies. These methods have different utilities for what researchers are trying to measure. Spurs of Impatiens flowers measured by Young (2008), for example, can be directed at multiple angles from the corolla of the flower. Angle of declension of the spur (and not curvature!) is what researcher are measuring. Similarly, angle of declension would apply to the hooks on the bills of Diglossa flower piercers and some hummingbird species (Glaucis, Ramphodon). Researchers need to decide what is most appropriate for their organism and define it as such.

*“The authors' method is assessing shape”.* **> We’ve defined *shape* (sensu Bookstein 1991) in the section “History of measuring curvature in pollination ecology”. Our method is assessing *curvature*, not shape. Curvature information is extracted from “shapes” but there is not quantification of shape in the geometric morphometric sense.**

**> We agree with** *“Angle of declension of the spur (and not curvature!) is what researcher are measuring.”.* **However, Young (2008) use it as a proxy for curvature, which is what this manuscript is advocating against.**

**> We agree with** *“Researchers need to decide what is most appropriate for their organism and define it as such.”***. One of the goals of this paper is to clearly define *curvature* so that these decisions are easier to make.**

Reviewer #2  
  
**Comment #1:** Although I really liked the literature review by the authors, I had questions the fact that some methods were not included in this discussion and were cited only later in the manuscript.  For instance, at lines 361-367, the author mention for the first time some examples of applications of geometry to measure curvature. Also, at the end of the manuscript (lines 491-493), the authors mention that MOMOCS offers an point-wise curvature estimation approach. Why does this come so late in the manuscript? It should be introduced in the intro. I would have liked to hear more about it since it seems very similar to the approach of the authors and I would have liked to see it compared in the empirical example.

*“..at lines 361-367, the author mention for the first time some examples of applications of geometry to measure curvature”.*

**> We have mentioned this already at line 293-295. The examples at lines 405-410 (previously 361-367) are reiterations and expansions on the point made at lines 293-295. We omitted these from the section “History of measuring curvature in pollination ecology” because they are examples from outside of this field, and the focus of the manuscript is to address a conceptual and methodological issue in pollination ecology specifically.**

*“..at the end of the manuscript (lines 491-493), the authors mention that MOMOCS offers an point-wise curvature estimation approach. Why does this come so late in the manuscript? It should be introduced in the intro. I would have liked to hear more about it since it seems very similar to the approach of the authors and I would have liked to see it compared in the empirical example.”*

**> As it stands, the introduction serves to illustrate the role that curvature (as an ecological concept) has played in pollination biology and testing theories from evolutionary ecology. Within MOMOCS, the function `coo\_tangent\_angle()` does have some similarities to the proposed point-wise definition of curvature. I’ve pasted the code from `Momocs:::coo\_tangent\_angle.default` here in case it is of interest:**

**1. p <- nrow(coo)**

**2. tangvect <- coo - rbind(coo[p, ], coo[-p, ])**

**3. tet1 <- Arg(complex(real = tangvect[, 1], imaginary = tangvect[, 2]))**

**4. tet0 <- tet1[1]**

**5. t1 <- seq(0, 2 \* pi, length = (p + 1))[1:p]**

**6. phi <- (tet1 - tet0 - t1)%%(2 \* pi)**

**7. return(phi)**

**The major limitations of this function are:**

**1) This function computes tangent angles *p* – 1 times, where *p* is the number of landmarks and semi-landmarks. For most morphometrics datasets, *p* landmarkswill not sample the shape of the specimen nearly enough to give a reliable approximation of *K*tot.**

**2) The function appears to be intended for closed outlines. Part of Line 2 re-arranges the order of the xy coordinates so that the last *xy* coordinate is subtracted from the first. This gives inaccurate curvature estimates for open outlines. E.g. running coo\_angle\_tangent() for coordinates plotted along a quarter unit circle gives 310.45 radians (should be ~1.57 radians).**

**3) This function computes phi for each landmark, but point curvature is (approximately) the rate of change of these values.**

**We realize that from a coding perspective, these three differences are relatively trivial, but together, the conceptual differences between this MOMOCS function and our definition of curvature are substantial. Based on these three points, we recommend the modified version of this function called `curvature\_tangle()` in `curvr` v.0.1.0 (github.com/mannfred/curvr).**

*“..I would have liked to see it compared in the empirical example.”*

**> For the reasons stated above, the tangent angle function from MOMOCS would not be appropriate for analysing total curvature in the *Epimedium* dataset.**

**Comment #2:** I was not able to fully understand the section on the definition of the method. I am not an expert in geometry or mathematics, but I would say I am above the average for a biologist and if I don't understand, I am afraid it will be difficult for many. Perhaps there is only a need to better define different terms and take time to explain all the formulas?  
  
Line 281-286: Maybe there is something I don't get, but it does not seem possible to define a segment with only two (x, y) coordinates. You either need to add a length and direction or a terminal point to define it. Is it because there is a parametric function defining the curve itself? In don't understand.  
  
Line 287: The authors mention arc length, but according to the figure, it is more a segment. An arc is a curved segment, but this is not what delta s is on the figure. Maybe I don't get the distinction between r and s? More explanation might be useful in this section.

*“The authors mention arc length, but according to the figure, it is more a segment.”***.** **These concepts are related but distinct: while arc length (*s*) is the length of the entire curve, we also use arc length *segments* (Δ*s*)as the intervals for the point-wise curvature estimates (lines 326-327).The curve is modelled by a function parameterized by *s*, while point-curvature is calculated at increments of Δ*s*.**

*“An arc is a curved segment, but this is not what delta s is on the figure.”* **Agreed. Δ*s* is a straight line that when taken to the limit (Δ*s* ­-> 0 = d*s*), approximates the curved segment of an arc (line 332).**

*“Maybe I don't get the distinction between r and s?”* **We define r at line 321 as a function of *s*. They are related, but whereas *si* gives us the *arc length* of a curve at point *i*, r is a *function* that outputs *xy* coordinates of a curve depending on the value of *s*.**

**Comment #3** I find that too few details are given on how to apply the methods (starting at line 353). How many landmarks? How to apply the mathematical function? Could we just resample the curve using equidistant points instead of using a function?

*“How many landmarks? “.* **The** **protocol is necessarily broad to accommodate the breadth of applications. E.g. we cannot advise how many landmarks will be necessary for every study organism and system. For brevity, this manuscript assumes that readers are already familiar with the basic principles of GM, or that they have taken our recommendation to read the primer cited at line 259. For more practical considerations, (e.g. guidelines for landmarking, sources of error) we have added two references for further reading at line 394. However, we agree that we could include more practical information regarding the methods used in the *Epimedium* study and have included a mention of the number of landmarks used in at lines 457-458.**

*“How to apply the mathematical function?”***. Similarly, this will depend on the shape of the study organism. We have pointed the reader to the geometric morphometrics literature which discusses the numerous options for fitting curves to landmarks (Rohlf 1990; Macleod 1993; Terral 2004) at lines 418-423.**

*“Could we just resample the curve using equidistant points instead of using a function?”* **Possibly. It depends on the study organism and number of semi-landmarks. One could iteratively re-sample until the semi-landmarks are extremely dense, but at that point, one could have simply fit a curve to fewer semi-landmarks and have the continuous function needed to compute derivatives from.**

**Comment #4:** Example scripts should be made available to show how to apply the proposed method (line 372-386). Also, although I asked for supplementary materials, I never got access to the script and data. This is unfortunate. This should be made available for proper review in a next round and made accessible if the paper is published.

**Agreed. We have created a Dryad submission (with all scripts and data) for the revised version.**

**Link for reviewers:** <https://datadryad.org/stash/share/H6-pYak3rTA2ohDrmZSl7cf4zYO9UZ-oqNVEKXdWIug>

**Comment #5:** The main complaint I have with the example is that there are too many distractions and the most important information is not made clear enough. I think the example is most useful in the context of this study to show (1) how to calculate the curvature (describing protocols and giving example scripts) and (2) to compare the proposed approach with previous ones. This is what should be shown in the main manuscript. All other results (morphospace, effect of the developmental stages and species) are of less importance and could be moved to the supplementary materials. Figure S7 and Tables S8 and S9 should be in the main manuscript. Figures 4 and 5 are not necessary, but figure 4 could be kept in the manuscript to show the variation in the studied organisms.

*“I think the example is most useful in the context of this study to show (1) how to calculate the curvature (describing protocols and giving example scripts) and (2) to compare the proposed approach with previous ones.”* **Agreed. The new version has restructured this section to emphasize the R protocol and a comparison with the older methods (starting at line 436).**

*“Figure S7 and Tables S8 and S9 should be in the main manuscript.* *Figures 4 and 5 are not necessary***..”. Figure S7 has been moved to the main text as Figure 5, though Tables S8 and S9 remain in the Supplementary Materials as we are limited to six (total) Figures and Tables. Figure 5 (now Figure 4 in the new version) shows that our total curvature metric can be used to test qualitative descriptions of shape space axes. This is significant because our curvature metric re-purposes the landmarks from the morphometrics protocol, so it represents shape information encoded within standard GM practices. For this reason we have kept it in the main text.**

**Comment #6:** Also, I don't understand why so much importance is given to geometric morphometrics. In the regression, curvature is not tested directly (as response variable) and only used to measure correlation with the PCs. Also, why was the trajectory analysis is done on the geometric morphometric (GM) data and not the curvature? This is strange given the subject of the study. Similarly, the authors cite figure 4 to describe curvature (line 417), but this figure only has GM data and no curvature measurements.

*“..I don't understand why so much importance is given to geometric morphometrics.”* **We agree that the previous version had too much of a focus on GM in the *Epimedium* demonstration. We have reduced this aspect significantly and focused instead on the comparison of the previous metrics. Nonetheless, GM is the standard for shape analysis and is widely used throughout evolutionary ecology. Therefore, we have left in a discussion of the relevance of the curvature metric to GM analyses, and illustrated its utility via Figure 4.**

*“In the regression, curvature is not tested directly (as response variable) and only used to measure correlation with the PCs.”* **Thank you for catching this omission. We have amended this issue at lines 472-473 (main text), with further information at lines 130-137 in the Supplementary Materials.**

*“Also, why was the trajectory analysis is done on the geometric morphometric (GM) data and not the curvature?”.* **We performed the trajectory analysis (TA) to demonstrate common practices in GM and how our curvature metric might compliment these analyses. Given that the new version will not focus on the TA, we have simply moved these results to the Supplementary Materials.**

*“Similarly, the authors cite figure 4 to describe curvature (line 417), but this figure only has GM data and no curvature measurements.”* **This raises a good point with regards to the limitations of GM – we mention this in the section “History of measuring curvature in pollination ecology”. At line 464 we write “The deformation grids illustrating variation in PCA shape space *suggested* that floral curvature increased along both PC1 and PC2.” which is where most GM analysis must end. We extend the GM analysis by calculating curvature directly from the landmarks used to quantify shape, which we hope is one of the major contributions of this manuscript.**

**Comment #7:** Line 403: What is section 4? There are other such mentions of sections elsewhere in the manuscript. Also, more information is needed here. How many landmarks? Were the points resampled along the curve? I would have liked to see the R scripts.

**Thank you for finding this mistake. A previous version had numbered sections. We have removed this in the newest version. The other comments regarding R scripts have been addressed above.**

**Comment #8:** It is really important to report effect sizes for the linear models (e.g., line 438) as p-values alone are by themselves not completely informative of the relationships.

**Agreed and completed. We’ve included ηp2 for the linear mixed models at lines 486-487, where ηp2 (partial eta squared) is an estimate of the variation in PC2 explained by total curvature (further detailed at lines 135-137 and 161-162 in the Supplementary Materials).**

**The results presented from lines 489-492 are from a pairwise comparison of means (Tukey’s HSD) and the effect size (difference in estimated marginal means) is written within the prose.**

**For the pairwise comparisons of the various curvature metrics (lines 500-504) we have reported Spearman’s rank order coefficient (ρ), which is a nonparametric measure of correlation for two monotonic variables (essentially effect size).**

**For the linear regression of “circle fit” and “residuals of 1/R and Ktot” (lines 504-506), we’ve reported ηp2 (as above).**

**Comment #9:** Why not show the regression slopes on figure 5?

**Agreed and completed. Note that this figure has been renamed as “Figure 4”.**