The inside curve{:} geometry and pollination ecology of curved flowers

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The curvature of a flower along the lateral plane ('floral curvature') is a widespread, convergent trait with important ecological and evolutionary implications. This review summarizes the methods used to measure floral curvature, suggests a clarification of the definition of curvature and a translation into a field-portable methodology. Intuitively, curvature is the degree to which a line is not straight. In plane geometry curvature is defined as 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 a lateral image of an organism, then computing curvature at many points along the fitted line and taking the sum. The utility of this metric was tested by studying the development of nectar spur curvature in *Epimedium* (Berberidaceae). Differences in the development of floral curvature were detected between *Epimedium koreanum* and *Epimedium grandiflorum* var. *violaceum*. Inflection points are found in wild-type *Epimedium grandiflorum*, but are lost in the cultivated variety '*violaceum*', resulting in loss of total curvature. The suite of functions used to quantify floral curvature in this study are available as an open-source R package 'curvy'. The major advantages of this method are 1) precision of measurement is increased without introducing expensive field equipment or computing power, 2) precision of terminology within pollination ecology is improved by adopting from the existing mathematical tools for studying line-curves, and 3) the opportunity is opened for investigating the genetic basis of (lateral plane) curvature measured at the cellular scale.

curvature | flower | corolla | hummingbird | pollination

The ecology of floral 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?" – **?**.

At the center of plant-pollinator diversification is a remarkable variety of floral form. The notion that plant communities are under selection to reduce interspecific mating ('floral isolation', **?**), points to the importance of floral diversity in initiating and reinforcing reproductive isolation (**?**). For example, in the rapid radiation of Andean *Centropogon* (Campanulaceae), competition for pollination led to the divergence of floral traits associated with bat and hummingbird pollination (**?**). Meanwhile, in South African *Lapeirousia* (Iridaceae), geographic variation in floral tube length has initiated reproductive isolation between morphs with short and long flower tubes, despite sharing the same fly pollinator (**?**). Thus, floral morphology is a key phenotypic feature underlying the diversification of plants and pollinators (**??**).

Flower-pollinator curvature as viewed from the side (lateral plane), has been a trait of special interest since the post-Darwin era of pollination ecology. In making pollinator observations of the Cape flora, Scott-Elliott (**?**) noticed that the flowers of *Leonotis ocymifolia* (Lamiaceae) visited by *Nectarinia* sunbirds were "curved with the same curvature as that of the bird's beak." (p. 272). Robertson (**?**) insightfully notes that the curved nectar spurs of *Viola* spp. (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. And these expectations have largely been supported: Stiles (**?**) first posited that neotropical *Heliconia* partition hummingbird 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 (**?**): along the slopes of the Central Cordillera (Costa Rica), the degree of flower-hummingbird bill curvature is proportional to plant-pollinator interaction strength (**?**) and extent of specialization (*d'*, (**?**). More recently the scope of plant-pollinator research has expanded to address the biogeography of curvature. As predicted by Stiles (**?**), Maglianesi *et al* (**?**) and Sonne *et al* (**?**) find curvature to be most prevalent in the lowland environments of the neotropics. Explanations for this pattern range from heightened competition at lower elevations to environmental filtering in the Andean highlands (**??**). Because the neotropical hummingbird subfamily Phaethornithinae comprises the majority of species with curved bills, we might expect plant-hummingbird curvature to have a predictable global distribution.

Pollinator specialization has major effects on macroevolutionary and biogeographic patterns (**???**), and curvature is a component, but widespread feature of specialist systems. Therefore, to synthesize our knowledge of curved plant-pollinator systems, curvature is a concept that needs an exact definition and method of measurement. In this review we summarize the approaches to measuring curvature within the field of plant-hummingbird pollination, identify strengths and shortcomings, and offer a solution with the aim of standardizing how curvature is studied within the field of pollination ecology. Although this review is motivated by the problem of measuring curvature in plant-hummingbird systems, the solution is general to any biological form modelled as a line curve: this case is hopefully made in the demonstration to follow.

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Document Options. We support several options via the YAML header

- Setting a DOI or URL footer, for example for the CRAN package URL, which is placed in the bottom-left footer of the title page and even pages;

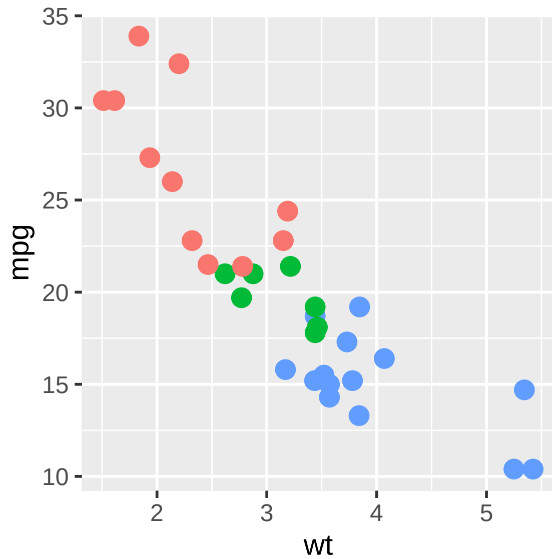

Fig. 1. Narrow ggplot2 figure

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References. Here we differ from PNAS and suggest natbib. References will appear in author-year form. Use `\citet{}`, `\citep{}`, etc as usual.

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Inline R Code. The PNAS sample included a fixed PNG image here, but this document prefers to show the results and embedding of *R* code.

```
library(ggplot2)
```

```
#  Warning: package 'ggplot2' was built under R version 3.5.3
```

```
ggplot(mtcars, aes(wt, mpg)) +
    geom_point(size=3, aes(colour=factor(cyl))) +
    theme(legend.position="none")
```

Here we use a standard knitr bloc with explicit options for

- figure width and height (`fig.width`, `fig.height`), both set to three inches;
- whether the code is shown (`echo=TRUE`); and
- the caption (`fig.cap`) as shown above.

Digital Figures. Markdown, Pandoc and LaTeX support `.eps` and `.pdf` files.

Figures and Tables should be labelled and referenced in the standard way using the `\label{}` and `\ref{}` commands.

The R examples above show how to insert a column-wide figure. To insert a figure wider than one column, please use the `\begin{figure*}...\end{figure*}` environment.

One (roundabout) way of doing this is to *not* actually plot a figure, but to save it in a file as the following segment shows:

```
library(ggplot2)
```

```
#  Warning: package 'ggplot2' was built under R version 3.5.3
```

```
p <- ggplot(data = midwest,
            mapping = aes(x = area,
                          fill = state,
                          color = state)) +
    geom_density(alpha = 0.3)
## save to file
suppressMessages(ggsave("densities.pdf", p))
```

This file is then included via standard LaTeX commands.

Typeset Code (But Do Not Run It). We can also just show code.

```
xx <- faithful[,"eruptions"]
fit <- density(xx)
plot(fit)
```

This simply used a pandoc bloc started and ended by three backticks, with `r` as the language choice. Similarly, *many* other languages can be typeset directly simply by relying on pandoc.

Single column equations. Authors may use 1- or 2-column equations in their article, according to their preference.

To allow an equation to span both columns, options are to use the `\begin{figure*}...\end{figure*}` environment mentioned above for figures. The `\begin{widetext}...\end{widetext}` environment as shown in equation **??** below is deprecated, but LaTeXcommands `\onecolumn` and `\twocolumn` work fine.

Please note that this option may run into problems with floats and footnotes, as mentioned in the cuted package documentation. In the case of problems with footnotes, it may be possible to correct the situation using commands `\footnotemark` and `\footnotetext`.

$$\begin{aligned}(x+y)^3 &= (x+y)(x+y)^2\\ &= (x+y)(x^2+2xy+y^2)\\ &= x^3+3x^2y+3xy^3+x^3.\end{aligned} \qquad [1]$$

Acknowledgments. acknowledgements go here

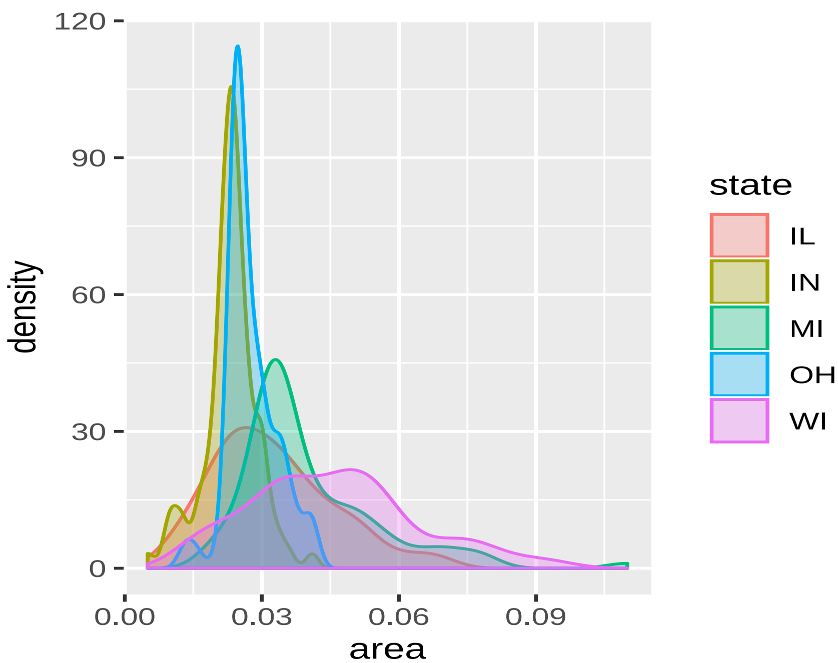

Fig. 2. Wide ggplot2 figure