Floral development in an Andean bellflower (*Centropogon granulosus*, Campanulaceae) and pollination by Buff-tailed Sicklebill (*Eutoxeres condamini*)

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#### Author Contributions

M.B. and Q.C. designed the study and D.A., J.J., and M.B. conducted the field work. M.B. analysed the data and wrote the first manuscript draft. All authors contributed to writing and editing the final manuscript.

#### Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article.

#### Introduction

   Plant-pollinator co-evolution is an important biotic driver of rapid Andean radiations. During Andean orogeny, numerous angiosperm clades diversified as they migrated and adapted to novel montane environments ([Gentry, 1982](#ref-gentry_1982)). In vicariant populations floral traits may drift, evolve via pleiotropy, or adapt to a pre-existing pollinator community ([Harder and Johnson, 2009](#ref-harder_2009); [Smith, 2016](#ref-smith_2016)). Subsequently, divergence in floral phenotype can be reinforced when reciprocal adaptation between the plant and pollinator promotes floral isolation ([Grant, 1949](#ref-grant_1949); [Thompson, 2005](#ref-thompson_2005)). This process is generally framed as special case of ecological speciation ([Gómez et al., 2009](#ref-gomez_2009); [Althoff et al., 2014](#ref-althoff_2014)), and is increasingly supported as a critical component of Andean floristic diversity (e.g. in *Costus* L. [Kay et al., 2005](#ref-kay_2005); *Lupinus* L. [Hughes and Eastwood, 2006](#ref-hughes_2006); bromeliads [Givnish et al., 2014](#ref-givnish_2014); centropogonids [Lagomarsino et al., 2016](#ref-lagomarsino_2016); epiphytic orchids [Pérez-Escobar et al., 2017](#ref-perez_2017)). However, while phenotypic and phylogenetic evidence generally supports the model of co-evolutionary diversification, the underlying microecological processes (sensu [Dellinger, 2020](#ref-dellinger_2020)) are comparatively understudied. For example, while a macroevolutionary model might detect the correlated evolution of floral traits and pollination mode, there is a need to ‘close the loop’ by testing these predictions in the field via studies of pollination ecology.

   Here we investigated whether microecological processes (i.e. biotic interactions, floral development) support the theory of pollinator-mediated speciation in the mega-diverse Andean bellflowers (Campanulaceae). *Centropogon* C.Presl, with *Siphocampylus* Pohl and *Burmeistera* H.Karst & Triana form a South American clade of Lobelioideae known as the ‘centropogonids’ ([Lagomarsino et al., 2014](#ref-lagomarsino_2014)); a clade arising in the last five million years and diversifying into over 550 species ([Lagomarsino et al., 2016](#ref-lagomarsino_2016)). This rapid radiation has been attributed to increased speciation rates driven by Andean uplift and the repeated evolution of hummingbird and bat pollination ([Lagomarsino et al., 2017](#ref-lagomarsino_2017)). The Andean clade *Centropogon* section *Centropogon* ([McVaugh, 1949](#ref-mcvaugh_1949)) or ‘eucentropogonids’ (38 spp., [Lagomarsino et al., 2014](#ref-lagomarsino_2014)) are distinct because of their elongated, hook-shaped flower tube, and the presence of a scale made of fused hairs that serves as a lever to deposit pollen (Figure S1). Both traits are thought to be adaptations for pollination by Sicklebill hummingbirds (*Eutoxeres*): two species of large Hermits (Phaethornithinae) named for their dramatically curved bill (Figure 1). In addition to eucentropogonids, the unique bill shape of *Eutoxeres* matches the curved flowers of *Heliconia* subgen. *Stenochlamys* Baker and *Heliconia* subgen. *Griggsia* L.Andersson (Zingiberales). The Hermits diverged early in the evolutionary history of hummingbirds (~26 Ma, [McGuire et al., 2014](#ref-mcguire_2014)), and represent one of two major hummingbird ecotypes: the trapliners (cf. territory holders, [Janzen, 1971](#ref-janzen_1971)). *Eutoxeres* diverged 21.5 Ma, and probably co-evolved extreme curvature within lowland Amazonia, before the uplift of the Andes ([Stein, 1987](#ref-stein_1987); [Abrahamczyk et al., 2017](#ref-abrahamczyk_2017)). During a recent period of major Andean uplift (~5 Ma) *Centropogon* colonized and radiated into novel montane habitat, with eucentropogonids evolving floral traits for pollination by *Eutoxeres* ([Lagomarsino et al., 2017](#ref-lagomarsino_2017)). This may have meditated the elevational expansion of *Eutoxeres*, and explains their persistence beyond the range of *Heliconia* ([Stein, 1987](#ref-stein_1987); [Abrahamczyk et al., 2017](#ref-abrahamczyk_2017)). At present, *Eutoxeres* has the largest elevational range of any Hermit hummingbird — it can be found in its ancestral range, the Amazonian lowlands, as well as the foothills and montane forests of the Andes up to 3300 m ([Hinkelmann and Boesman, 2020](#ref-hinkelmann_2020)). However, the physiological pre-adaptations that allowed Sicklebills to expand upslope, and not other Hermits, remains unknown ([Stiles, 2004](#ref-stiles_2004)).

   Recent work has supported the divergence of eucentropogonids coincident with adaptation to Sicklebill pollination ([Lagomarsino et al., 2017](#ref-lagomarsino_2017)). One of the hypotheses generated by this finding is that eucentropogonids are pollinated by White-tipped Sicklebill (*Eutoxeres aquila*, Costa Rica to northern Peru) or Buff-tailed Sicklebill (*E. condamini*, northern Peru to Bolivia). Indeed, previous studies have progressively supported White-tipped Sicklebill as a specialized pollinator of *Heliconia* and eucentropogonids: this hummingbird is known to be a trapliner ([Stiles, 1985](#ref-stiles_1985)), it pollinates the aforementioned plants ([Gill, 1987](#ref-gill_1987); [Maglianesi et al., 2015](#ref-maglianesi_2015); [Morrison and Mendenhall, 2020](#ref-morrison_2020)), and network analyses of plant-hummingbird communities indicate that its curved bill contributes to niche partitioning ([Maglianesi et al., 2014](#ref-maglianesi_2014); [Sonne et al., 2019](#ref-sonne_2019)). In contrast, very little is known of its southern congener, *E. condamini*. Thus, the goal of this study is to further test the theory of pollinator-meditated diversification in the eucentropogonids by examining the microecology of the Andean bellflower *Centropogon granulosus* C.Presl and Buff-tailed Sicklebill in the cloud forests of southeastern Peru. We structured our approach by asking (1) Do phenological traits in *C. granulosus* support the morphological evidence for Sicklebill pollination? (2) Is Buff-tailed Sicklebill a visitor of *C. granulosus*? and (3) Does visitation affect the fitness of *C. granulosus*? While other eucentropogonid species are found in this region (Figure 1), here we focus on *C. granulosus* as it is locally abundant and presents a tractable system for study. *E. condamini* is the only Sicklebill species present at this latitude (see: Methods); its congener (*E. aquila*) occurs further north, from the Loreto region of northern Peru to the Cordillera Central of Costa Rica.

#### Materials and Methods

*Pollination Syndrome*

   We assessed the pollination syndrome of *C. granulosus* via literature search and measurement of additional floral traits, namely floral tube length and curvature. Landmarks and semi-landmarks were assigned to scaled photographs of *C. granulosus* using *tpsUtil* v1.76 ([Rohlf, 2015](#ref-rohlf_2015)). Landmark data was imported into R using the import\_tps() function from Momit vXXX ([**bonhomme\_2014?**](#ref-bonhomme_2014)) and fit with smoothing cubic splines using stats::smooth.spline(). Arc length and total curvature of each floral tube was estimated from the fitted splines using pracma v2.2.5 ([**borchers\_2019?**](#ref-borchers_2019)) and curvr v0.0.1 ([**boehm\_2021\_b?**](#ref-boehm_2021_b)).

*Field Site and Local Flora*

   We based our field work at the Gallieto de las Rocas Lodge, San Pedro, situated at ~1400 m a.s.l in the Kosñipata Valley, Peru (-13.055, -71.548 DD, Figure 2). Research Permit No. 0441-2017 was administered by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR).

To estimate local patterns of occurrence, we searched Tropicos v3.2.2 ([**missouri\_2021?**](#ref-missouri_2021)) for *Centropogon* and *Heliconia* species documented within the Kosñipata Valley. We used the species list to query the Global Biodiversity Information Facility (GBIF) for continent-wide occurrence records via the rgbif package vXXX ([**CITATION?**](#ref-CITATION)). Elevation was estimated from latitude-longitude data (precision = 30m x 30m) associated with the GBIF records using rgbif::elevation().

*Pollinator Observations*

   In this study, we deployed five camera traps (Reconyx Hyperfire HC600) near *Centropogon granulosus* vines located in a previous survey of the area ([Boehm et al., 2018](#ref-boehm_2018_a)). Camera traps were checked for new captures every 24 hours. If no floral visitors were recorded within three days, the camera traps were moved to different *Centropogon* individuals. Where floral visitors were recorded, we attempted targeted (manual) video recording to better document visitation behaviour. Camera traps were active continuously from August 17 to September 20, 2017. Monitored locations are listed in Table S1.

*Pollinator Exclusion Experiment*

   Following the methods of Sun et al. ([2017](#ref-sun_2017)), we constructed and deployed wire cages covering one inflorescence each from six *Centropogon* individuals (Figure S2). Wire cages prevent hummingbirds from contacting the flowers while allowing invertebrates to move freely. An additional ten inflorenscences were tagged and monitored as controls. Using the control flowers, we defined four stages of floral development (Table 1). These stages were used to quantify and compare the developmental trajectories of the control and pollinator-excluded flowers. Monitoring of a flower stopped when 1) berry development completed (stage E), 2) the flower died prematurely, or 3) the study period ended. Daily observations were recorded between August 17 and September 20, 2017. Floral development data was analysed in R v4.0.2 ([R Core Team, 2017](#ref-R_2017)) and organized using here v0.1 ([Müller, 2017](#ref-muller_2017)) and tidyverse v1.3.0 ([Wickham et al., 2019](#ref-wickham_2019)) . All data and R scripts are available as an RStudio Project [XXX] hosted at github.com/mannfred/centropogon.

   Flowering stage data was staggered because each flower developed independently. The data was also fragmented because some samples abscissed prematurely due to herbivory or weather. This type of data was treated as ‘right-censored,’ i.e. some flowers exited the study before reaching maturity ([Allison, 2014](#ref-allison_2014)). Similarly, we collected data from flowers that had already progressed past the initial stages (‘left censored’). Although manually aligning the developmental data is possible, for convenience we used a multiple sequence alignment protocol to automate the process. To do this, we first pruned the sequence fragments into ‘early’ (stages A and B) or ‘late’ (stages C and D) types. We then aligned all fragments of one type through ClustalW implemented in the R package msa v.3.9 ([Bodenhofer et al., 2015](#ref-bodenhofer_2015)) with a neutral (identity) substitution matrix. Aligned sequences were then used to compute a consensus sequence for the ‘early’ and ‘late’ stages — this was done using the ConsensusSequence() function in DECIPHER v2.14.0 ([Wright, 2015](#ref-wright_2015)). The consensus was computed with a 15% threshold (the maximum proportion of sequences not represented at any given position). The consensus ‘early’ and ‘late’ sequences were then spliced to give the full consensus sequence of floral development. This process was repeated separately for both the control and pollinator-excluded data.

   We conducted an event history analysis ([Allison, 2014](#ref-allison_2014)) to compare the probability of post-anthesis survival between pollinator-excluded and control flowers. First, we counted the number of days elapsed from anthesis (Stage C) through berry development (Stage D) for each flower (), and pooled the data for control ( = 61) and pollinator-excluded ( = 29) plants. Daily survival probability (from anthesis) was calculated for each treatment using the survival package v3.1 ([Therneau, 2015](#ref-therneau_2015)). Differences in survival probability were evaluated by a log-rank test ([Peto and Peto, 1972](#ref-peto_1972)) using the survdiff() function in the above R package.

*Flowering mode*

To model flowering phenology of *C. granulosus*, we fit linear models to the rate of anthesis and senescence for each inflorescence that produced at least five flowers ( = 6 controls, = 5 pollinator excluded). We also examined whether pollinator-exclusion affected flower production and the timing of the male and female phases of anthesis. Model fits were evaluated in broom v.0.7.6 ([Robinson et al., 2021](#ref-robinson_2021)), Hedge’s weighted effect sizes () were calculated in effectsize v0.4.4 ([Ben-Shachar et al., 2020](#ref-shacar_2020)) and trait variation was quantified by the stats::aov() function in R. Models are further described in the Supplementary Materials.

#### Results

*Pollination syndrome*

From the literature search, we assigned values to X aspects of the *C. granulosus* pollination syndrome (Table SXXX). By organizing the traits hierarchically, we can reasonably hypothesize that *C. granulosus* is hummingbird-pollinated. By adding additional traits measured in this study, the pollination syndrome suggests pollination by *Eutoxeres*. With this in mind, we examine additional lines of evidence below.

*Local patterns of occurrence*

*Floral development and pollinator exclusion*

Results:

# flowers produced over lifespan of experiment

# flowers open on average

* flowering rate (linear)
* abscission rate (linear?)
* male vs female duration
* include nectar robber frequencies in table 2?
* a ‘syndrome’ table? with qualitative and quantitative traits,
* we then add three lines of evidence to narrow down the most likely pollinator. exclusion = hummingbird geography = BTS (Species) observations = (Species)
* qualitative observations re: curvature development. We did a post-hoc analysis of curvature development using only the reference photographs taken for the characterization of life stages (see: Table XXX).

   Hummingbird-exclusion did not affect the number of flowers produced (df = XXX, = 0.91). Caged inflorescences produced 11.2 ± 4.6 flowers whereas controls produced 12.2 ± 8.1 flowers (mean ± standard deviation). We note that these numbers reflect flowering over the lifespan of the experiment; the upper limit of flower production for a single inflorescence is not known, though we counted up to 68 peduncle scars on an individual not included in this study (Figure S3). While *C. granulosus* flowers generally open sequentially, temporal overlap is not uncommon (Figure XXX). However, the average number of flowers open on pollinator-excluded individuals (1.58 ± 1.14) was greater than the controls (0.84 ± 1.22, = 0.0003, = 0.62). **NEED RANDOM EFFECT FOR INDIVIDUALS**

Linear models accurately described flowering rate (Figure XXX): the mean and standard variation adjusted was 0.934 ± 0.047, with minimal variation in between individuals (df = XXX, = 0.301. Flowering rate did vary between individuals (df = XXX, = 0.037), but not between treatments (df = XXX, = 0.267). The flowers of *C. granulosus* are dichogamous, and pollinator exclusion did not affect the onset or duration of either phases ( = 1.3, = 0.181, Figure XXX).

   We identified and described four discrete stages of floral development in *C. granulosus* (Table 1). Delimiting floral development into four stages generated a consensus developmental sequence that mapped at least 85% of the sequence data collected in this study. These four stages were used to compare differences in development between control and pollinator-excluded flowers. From the floral phenology data we estimated consensus developmental sequences for each treatment (Figure 3). Between treatments floral development is comparable from stages A (bud development) to C (anthesis). However, control flowers spend an additional 18 days developing berries, while hummingbird-excluded flowers did not produce berries (Figure 3). Event history analysis showed that, following anthesis, daily survival probability decreased at similar rates. However, at 13 days post-anthesis, hummingbird-excluded flowers abscise, while control plants continued to produce berries (Figure 4). Overall, the survival curves differed significantly ( = 4.5, = 0.0336).

*Floral Visitors*

   Camera trap recordings and *in situ* observations confirm Buff-tailed Sicklebill as a visitor to *Centropogon granulosus* flowers (Figure 1, Figure S4, VIMEO). We recorded 12 visits to six *C. granulosus* individuals over 32 days (Table 2, Table S1). Visitation tended to occur from 5:20 to 10:40 in the morning (=9), and 12:40 to 16:30 in the afternoon (=3), though these patterns were likely affected by our own activity in the area, including mist-netting. A total of seven flowers were probed from six *C. granulosus* individuals, i.e. a second visit was recorded to an inflorescence as flowers opened sequentially. We observed feeding both by perching on the lignified inflorescence (=3), as well as hovering (=9). We also recorded two instances of Sicklebills approaching and inspecting inflorescences without open flowers. Wedge-billed hummingbird (*Schistes geoffroyi*) was also recorded nectar robbing *C. granulosus*; further details can be found in Boehm ([2018](#ref-boehm_2018_b)).

   Reviewing still frames from the video recording reveals an interesting feeding problem posed by the sharply curved flowers of *C. granulosus*. The hook-shape forces the hummingbird to raise its head so that it is facing skyward in order to insert the tip of its bill into the flower aperture (Figure S4), the remainder of the bill is further inserted by tilting the head back to resting position. Due to the unique morphology and orientation of *C. granulosus* flowers, this maneuver is unlikely to be performed by any other hummingbird while hovering. [COROLLA INFLATION pg 11 of lagomarsino\_2018]

   Two additional vertebrates, a murid and a long-nosed bat (Glossophaginae) were recorded near the inflorescences, but not observed to interact with the plant directly (Figures S5, S6). We note this because it is unknown how the fleshy berries are dispersed. We did however document signs of partial frugivory (Figure S7).

   Numerous invertebrates occupied or visited the flowers of *C. granulosus* in this study. As found in previous studies, we observed ants ([Stein, 1992](#ref-stein_1992)), mites ([Naskrecki and Colwell, 1998](#ref-naskrecki_1998)), and dipterids ([Weiss, 1996](#ref-weiss_1996)) in or on the flowers of this species. Though *Anelosimus* spiders (Araneae) are known to build webs scaffolded by *Centropogon coccineus* (Hook.) Regel ex B.D.Jacks. ([Nentwig and Christenson, 1986](#ref-nentwig_1986)), we observed unidentified Aranids inside of the floral tubes. We also recorded an unidentified larval leptidoptran inhabiting a flower (Figure S8).

A fly stealing pollen (MVI\_1124.AVI)

#### Discussion

*Buff-tailed Sicklebill is a pollinator of* C. granulosus

   In this study we photo-documented Buff-tailed Sicklebill visitation to *C. granulosus*, and demonstrated that hummingbird visitation is required for berry development. We interpret the inability of hummingbird-excluded flowers to produce berries as owing to a lack of pollination.

*Centropogon* pollen collected from White-tipped Sicklebill (*Eutoxeres aquila*) has been identified in previous studies ([Maglianesi et al., 2015](#ref-maglianesi_2015)), including *C. granulosus* ([Morrison and Mendenhall, 2020](#ref-morrison_2020)). And while *Centropogon* pollen has been identified from Buff-tailed Sicklebills from this study site ([Dyck-Chan et al., 2021](#ref-dyck-chan_2020)), species-level pollen identification for *Centropogon* remains difficult. Confirmation of *C. granulosus* pollen on Buff-tailed Sicklebill (*E. condamini*) would help to bolster the evidence presented here.

*Steady State Flowering and Traplining*

*C. granulosus* exhibits a linear flowering rate befitting the ‘steady state’ ecotype described by Gentry ([1974](#ref-gentry_1974)). It is one of several phenological modes that are thought to have evolved via competition for pollinators, and represents an axis of niche partitioning that contributes to tropical plant diversity ([Gentry, 1974](#ref-gentry_1974); [Kessler et al., 2020](#ref-kessler_2020)). Indeed, most hummingbird species exhibit foraging behaviour that is adapted either to steady state or ‘cornucopia’ flowering (sensu [Gentry, 1974](#ref-gentry_1974)), with few species able or willing to visit plants of both types (reviewed in [Kessler et al., 2020](#ref-kessler_2020)).

The designation of ‘steady state’ implies a general mode of flowering, however the nuances of this strategy are not well known [XXX]. We note that several aspects of flowering were not affected by pollinator exclusion: the number of flowers produced, the rate of flowering, and duration of the male/female phases of anthesis. Conversely, pollinator-excluded plants tended to have more flowers open than the controls. Whether this suite of traits is adaptive (e.g. it improves chances of pollination), or incidental is an unexplored aspect of the steady state ecotype.

   Sicklebills were not marked in order to distinguish individuals, so our ability to comment on individual behaviour is limited. However, based on population estimates of other Hermit hummingbirds, we assume that the local *E. condamini* population is on the order of XXX. Considering the above, the camera trap records support the notion that Buff-tailed Sicklebill, like other Hermits, is a trapliner (sensu [Janzen, 1971](#ref-janzen_1971)). We make this designation based on the observations that 1) these hummingbirds have not been recorded defending static territories, and 2) individual food plants are visited 1-2 times per day for brief (seconds) periods of foraging or inspection.

Traplining is widely viewed as an adaptation to steady state flowering ([Kessler et al., 2020](#ref-kessler_2020)). Hummingbird traplines can reach several kilometers in length ([Volpe et al., 2014](#ref-volpe_2014)) and can increase pollen transfer between plants separated by similar distances ([Torres-Vanegas et al., 2019](#ref-torres_2019)). The large distances traveled by trapliners is suggestive of pollinator specialization (sensu [**XXX?**](#ref-XXX)). A synthesis of the morphological (e.g. bill shape), behavioural (e.g. foraging), and physiological (e.g. metabolism) traits commonly associated with specialization in hummingbirds would provide an exciting test of the ‘specialist syndrome’ concept.

Describing the traplines of *Eutoxeres*, and the consequent affects on *Centropogon* diversification are avenues yet explored.

Unlike other Hermit hummingbirds (e.g. *Phaethornis*), the Sicklebills we encountered were wary of human activity. On August 23, we mist-netted a single Sicklebill near *C. granulosus* for a separate study (Table 2); We suggest that the consequent shift from mid-morning to early-morning visitation is indicative of the ability for traplines to be modified, in this case to avoid human activity.

*Perching versus Hovering*

   In contrast to previous accounts of Sicklebill visitation to *Centropogon* ([Stein, 1987](#ref-stein_1987)), we observed hovering in addition to perching. As with other hummingbirds, they are adept fliers and appear to probe flowers with ease (VIMEO). While floral orientation in hummingbird-pollinated plants may have evolved to exclude non-hovering visitors [XXX], hovering is energetically expensive for hummingbirds and likely to be avoided when possible. Recent work by Colwell et al. ([2021](#ref-colwell_2021)) found that short-billed hummingbird species have repeatedly evolved claws that improve their ability to perch. Conversely, long-billed species tend to hover to feed, supporting the idea that long (and sometimes curved) tubular flowers evolve in response to selection for pollinator specialization (reviewed in [Boehm et al., 2021](#ref-boehm_2021_a)).

   We speculate that the inflorescences of *C. granulosus* are lignified primarily to support and orient flowers, and are only opportunistically used by Sicklebills as perches. This is because open flowers are, on the majority, oriented to face away from the stem on long peduncles (Figure SXXX). This is in contrast to Sicklebill visits to *Heliconia* made at the same study site: flowers are oriented so that the opening is on the same plane as the perch (the floral bract, Figure SXX).

Pleiotropy and advertisement traits vs efficiency traits

*Concluding Remarks*

   Confirming Sicklebill visitation in *C. granulosus* raises myriad questions. For instance, given that the eucentropgonid clade is so diverse and widespread in southeastern Peru (Figure 1), is *Eutoxeres* the pollinator of all of these species? Furthermore, what mechanisms, if any, prevent interspecific pollen transfer within this clade? Through the effort of making pollinator observations, we were surprised to learn that another hummingbird (*Schistes geoffroyi*) is a nectar robber of *C. granulosus* (described in [Boehm, 2018](#ref-boehm_2018_b)). An entire literature on the competitive interactions for nectar and effects on the focal plant offer many avenues for future research [XXX]. For example,

While the pollination syndrome concept is well-supported, empirical observations remain foundational to understanding the dynamics of plants-pollinator evolution ([Dellinger, 2020](#ref-dellinger_2020)). >>maybe insert the big Qs in this field?

At the heart of this study, and the many excellent investigations into this system, is the question “why and what are the mechanisms that select for and maintain extreme curvature in these plant and hummingbird clades?” and “what is the role (if any) of curvature in the rapid diversification of the eucentropogonids?”

# {r figure1, echo=FALSE, fig.cap="Figure 1. Distribution of \_Centropogon\_ and \_Heliconia\_ along the Manú Gradient, southeastern Peru. Data aquisition and analysis described in the Supplementary Materials.", out.width = '100%'} # knitr::include\_graphics(here("Figures/Figure\_1.jpg")) #

# {r figure2, echo=FALSE, fig.cap="Figure 2. A: Geographic context for study site in southeastern Peru. Coordinates are in decimal degrees. B: Montane cloud forests of the eastern Andes (San Pedro, Peru). C: Trait-matching in \*E. condamini\* and \*C. granulosus\*. D: Camera trap documentation of \*E. condamini\* pollinating \*C. granulosus\*.", out.width = '100%'} # knitr::include\_graphics(here("Figures/Figure\_2.tif")) #

# {r figure3, echo=FALSE, fig.cap="Figure 3. Effects of pollinator exclusion on floral development. Developmental stages are described in Table 1.", out.width = '100%'} # knitr::include\_graphics(here("Figures/Figure\_3.jpg")) #

# {r figure4, echo=FALSE, fig.cap="Figure 4. Effects of pollinator exclusion on survival probability.", out.width = '100%'} # knitr::include\_graphics(here("Figures/Figure\_4.jpg")) #

# {r figure5, echo=FALSE, fig.cap="Figure 5. Flowering rate in \_C. granulosus\_. The $x$-axis represents the number of days elapsed since the first flower opened. The $y$-axis counts the cumulative number of flowers opened since $t$=0", not the number of flowers open simultaneously.", out.width = '100%'} # knitr::include\_graphics(here("Figures/Figure\_4.jpg")) #

# {r include=FALSE} # knitr::opts\_chunk$set(echo=FALSE, warning=FALSE, message=FALSE) # #

# {r include = FALSE} # library(googlesheets4) # # # prevent using auto-token # gs4\_deauth() # # # sign in # gs4\_auth(email = 'mannfredboehm@gmail.com', # scopes = "https://www.googleapis.com/auth/spreadsheets") # # # my "app" info from https://console.cloud.google.com # google\_app <- httr::oauth\_app( # appname = "mannys\_cool\_app", # key = "1089626906814-9lggcl5o3m7oeaqr583bs23h8pkbdgl7.apps.googleusercontent.com", # secret = "2uIBhIcqOC85xMx5EWkdQGHG" # ) # # # my API key # google\_key <- gs4\_api\_key() # # # configure access # gs4\_auth\_configure(app = google\_app, api\_key = google\_key) # #

# {r table1} # # library(googlesheets4) # # table1 <- read\_sheet('1VzmXOzNcNKxmyFNfu\_fBt6eqI4MsqAt3XuXTVmFJhlo', col\_names=TRUE) # # knitr::kable(table1, caption = 'Table 1: Stages of floral development in unmanipulated \_Centropogon granulosus\_. Stage duration is reported from the consensus sequence estimation (see: Methods). Representative photos for each stage are included in Figure 3.') # #

# {r table2} # # library(googlesheets4) # # table2 <- read\_sheet('1H5q2QBCAGkAfGbFFi2p1YH\_5dOJTYvm-61Rotayau1A', col\_names=TRUE) # # knitr::kable(table2, caption = 'Table 2: Camera trap records of Buff-tailed Sicklebill (\*E. condamini\*) visitation at \_C. granulosus\_.') # #

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