



Pollination biology of four co-occurring *Erica* species from the Cape peninsula, South Africa

S. Ingram, 2011.

Abstract:

Although pollinators have been suggested to drive speciation in the Cape flora, this has not been tested for the largest, florally diverse Cape genus *Erica*. Speciation studies that focus on pollination biology often use floral syndrome characters to predict a species' functional pollinator group/s. The predictive power of these techniques has come under scrutiny, and hence in-situ observations have become highly important for confirming existing pollination syndromes. Here I performed pollinator observations and recorded various floral traits of four co-flowering, co-residing *Erica* species in the Kalk Bay mountains, South Africa. The predictive pollination syndromes were confirmed through direct observations in the field. *E. ericoides* and *E. glabella* subsp. *glabella* were confirmed as insect pollinated plants, and *E. plukenetii* subsp. *plukenetii* and *E. abietina* subsp. *atorosea* were confirmed as bird pollinated plants. Interesting correlations between floral traits and visitation rates are also suggested.

Introduction:

The Cape Floristic region, one of the six floral kingdoms of the world, has been viewed as a perfect model system for understanding the genesis of plant diversity (e.g. Linder, 2005; Schnitzler et al. 2011). This is owing to its extremely high endemism (67% of its species), species-richness (9000+ species) and large variation in the richness of its distinctive Cape floral clades (Linder, 2005). Many theories have been proposed to explain these remarkable characteristics of the Cape flora. First

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theories involved the Mid Miocene climate change (Goldblatt and Manning, 2000), however climate models could only explain half the observed richness (Kreft & Jetz, 2007). Thus numerous ecologically based driving forces, which could potentially cause reproductive isolation between sister species (van der Niet & Johnson, 2009, Schnitzler et al., 2011), were proposed as combined forces of speciation in the Cape.

One of these driving forces is the role that pollinators have had in speciation in the Cape (Johnson, 1996). Pollinator specialization has been suggested as a major driving force to speciation in Cape clades owing to the presence of many large, florally diverse genera with high levels of specialized pollination systems, often within groups of closely related groups (Linder, 2003). The genus *Erica* L. is the most species-rich genus within the extremely species rich Cape Floral Kingdom (Oliver et al. 1983) arguably making it the most important genus when considering the speciation of the Cape. Rebelo, Siegfried and Oliver (1985) categorized this highly diverse genus by their putative pollinating agents based on their floral morphology. They speculated how the shape of the opening, length of the corolla, and the position of the stamens defined how the plant is pollinated. However, there have been limited in-situ observations confirming these predictions; however they are treated as fact in the conclusions of a species' pollination syndrome (eg. Barnes et al., 1995, Turner & Conran, 2004, Potgieter & Edwards, 2005), evolution (Potgieter et al., 1999) or phylogeny construction (McGuire & Kron, 2005).

Floral traits such as colour, shape, rewards and scent are believed to reflect the foraging preferences and morphology of their pollinators (Faegri & van der Pijl,

1979). These “pollination syndromes” are believed to arise via pollinator-mediated selective pressures for more efficient pollen transfer (Stebbins, 1970), however predicting primary pollinators using these syndromes has come into doubt (Ollerton 1998; Hingston & McQuillan 2000) as in the field the predicted primary pollinators may play only minor roles in the reproductive success of the plant (Ollerton, 1998, Coetzee & Giliomee, 1985). However, it remains that these pollination syndromes provide great utility in understanding the mechanisms of floral diversification since it is highly important to organize pollinators into functional groups according to presumed similarities in the selection pressures they exert (Fenster et al. 2004), especially in species rich and florally diverse taxa. Rebelo et al.’s (1985) predictive categories therefore require observations. This project aims to test the predictions made by Rebelo et al. (1985) by coupling these with field observations of four co-flowering species of *Erica*, which are all found on the mountains behind Kalk Bay, Cape Town.

2. Methods

2.1 Study species

Erica glabella Thunb. subsp. *glabella* occurs in sandy or rocky places on the mountains and flats of the Cape Peninsula. This shrublet, consisting of dense branching with short, thin, smooth ericoid leaves, is covered in small, pink and slightly ovoid to tubular flowers (Fig. 1). Predicted as an insect pollinated, possibly wind pollinated plant (Rebelo et al. 1985).

Erica abietina L. subsp. *atrorosea* E.G.H.Oliv. & I.M.Oliv. (or *Erica phyllicifolia*) is one of seven subspecies (the others are subsp. *abietina* L., *constantiana* E.G.H.Oliv. & I.M.Oliv., *aurantiaca* E.G.H.Oliv. & I.M.Oliv., *diabolis* E.G.H.Oliv. & I.M.Oliv., *perfoliosa* E.G.H.Oliv. & I.M.Oliv., *petraea* E.G.H.Oliv. & I.M.Oliv.). It is commonly found on the rocky slopes and mountain tops of the Cape Peninsula as a one metre high shrub arising from a single woody stem with dense, dark green ericoid leaves. This heath has pink-purple flowers, slightly sticky to the touch and arranged in clumps at the end of branches. It flowers from December to August (Fig. 1). Predicted as a bird pollinated plant (Rebelo et al. 1985).

Erica plukenetii L. subsp. *plukenetii* is one of five subspecies (the others are subsp. *bredensis* E.G.H.Oliv. & I.M.Oliv., *breviflora* E.G.H.Oliv. & I.M.Oliv., *lineate* E.G.H.Oliv. & I.M.Oliv., *penicillata* E.G.H.Oliv. & I.M.Oliv.). It has a large distribution range, occurring on well drained, rocky or sandy mountain slopes and flats throughout the CFR. This one metre high shrub with long upwardly curved needle-like leaves, flowers almost all year round but mainly in late summer-winter-spring (March to September). It has red-pink long tubular flowers which hang downwards with long exerted anthers protruding far from the tube (Fig. 1). Predicted as a bird pollinated plant (Rebelo et al. 1985).

Erica ericoides (L.) E.G.H.Oliv. is found on the lower slopes of mountains on the Cape Peninsula. It is a sturdy shrub reaching 60cm in height, consisting of dense branching with short, fat, hairy, ericoid leaves. From January to June it is covered in dense

clusters of short white flowers (6 to 12 in an umbel), often reaching into their thousands and tens of thousands (Fig. 1). Predicted as an insect pollinated, possibly wind pollinated plant (Rebelo et al. 1985).

2.2 Study site

The study was conducted from May 2011 to September 2011 at a site on an eastern slope of the Kalk Bay mountain (34.119439 S, 18.44354 E) on the Cape peninsula, South Africa. The site is characterized by Table Mountain sandstone, on gradual rocky slopes, near a perennial stream. The populations of all four co-occurring and co-flowering species were abundant with approximately 40 or more plants per species.

2.3 Floral visitor observations

Since distinguishing between pollinators and visitors needs analyses of pollen loads and assessments of whether floral visitors transfer pollen grains to stigmas, we will refer to the potential pollinators as visitors. I used behaviour to distinguish between 'robbers' of nectar (without passing on/receiving pollen) and 'visitors' (potentially passing on/receiving pollen). Correct behaviour for a potential pollinator required regular and frequent visits (Faegri & van der Pijl, 1966). Similarly, correct entry into the corolla for a potential pollinator required a plausible mechanism to exist for both acquiring pollen on initial entry and transferring pollen onto the stigma of the next flower visited (Faegri & van der Pijl, 1966). These distinguishing habits were determined at an observational level. Visitors were then recorded and characterized

into functional groups that behave in similar ways on a flower (Fenster et al. 2004). These were either “large hymenoptera”, “small hymenoptera”, or “bird”.

2.4 Visitation rates

Observations involved observing 5 visitors of each plant species for up to ten-minute intervals (i.e. if a visitor left before ten minutes were up this would complete that plants’ observation, then a new plant would be observed until a new visitor arrived and the ten minute observation period would commence). While observing visitors, the total flowers visited per plant and the handling times of each plant by the visitor (expressed as seconds, up to ten minutes) were recorded. Average handling time of each flower was then calculated by dividing handling time of plant by total flowers visited. Each observation of a single visitor was conducted on a different plant, resulting in five different plants and visitor observations per plant species. The distance between observer and plant depended on whether flowers were visited by insects or birds. Observations were conducted on days with below 15 km/h wind speed to control for a-biotic factors.

2.5 Anther ring disturbance

Direct observations cannot capture all data, especially data that occurs when the observer is not present. Since Ericas have fused anther rings, when these rings are disturbed, the anthers release pollen (these broken anther rings are easily observed with a 10X handlens). Geerts and Pauw (2011) identified this as an easily quantifiable proxy for visitation rates. Therefore to achieve a broader idea of what occurs outside

of direct observations anther ring disturbance was taken into account. To compare each species' proportion of total flowers visited, anther ring disturbance was used as a proxy for visitation rates for each species. I thus recorded disturbance of anther rings for 50 flowers per plant on 20 plants for *E. abietina* and *E. plukenetii*, and 400 flowers per plant on 20 plants for *E. ericoides* and *E. glabella*.

2.6 Floral traits

To record the association between floral traits and floral visitors, flower morphology and colour were quantified. Both corolla length and width of the corollas narrowest opening were measured, to the nearest ten micrometers, on five randomly selected flowers of four plants per species using digital calipers. Number of flowers per plant was also estimated for each of the four study species, by counting 100 flowers and estimating how many similar sized bunches would fit into the remaining plant.

The spectral reflectance of the corolla petals (N=3 flowers from 4 plants) of all four species was measured using an Ocean Optics Jaz Modular Optical Sensing Suite spectrometer in the lab after correcting with both a black and white control.

To compare the visitation rates and floral traits between pollination syndromes and also between species, normality tests were performed before a one-way analyses of variation (ANOVA) was conducted on the visitation rates between all four species. A post-hoc Tukey HSD test was conducted to find out where the significant differences occurred. Total flowers had to be logged and the proportion of flowers visited had to be transformed using the arcsin square root function for normality. To determine if the floral syndromes predicted by Rebelo et al. (1985) can be confirmed, a nested

ANOVA test was performed with the four study species as the random variable and these nested within the pollination syndromes. These were conducted on total flowers per plant, corolla length and corolla opening measurements between the predicted insect pollinated *E. ericoides* and *E. glabella* subsp. *Glabella* (grouped) and also between the predicted bird pollinated *E. plukenetii* and *E. abietina* subsp. *atrorosea* (grouped) (Rebelo et al., 1985). To compare the floral traits between species within each predicted syndrome, a post-hoc Tukey HSD test was conducted to find out where the significant differences occurred, these were then compared to the visitation rates.

3. Results

3.1 Visitor observations

The flowers of *E. plukenetii* were visited by a range of insects (including bees, ants and flies), in addition to the orange-breasted sunbird (*Anthobaphes violacea* L.) (Table 1). Bees and the orange-breasted sunbird were the most frequent visitors. The flowers of *E. abietina* were visited frequently by both a small wasp and the orange-breasted sunbird (Table 1). The small flowers of *E. glabella* and *E. ericoides* were both visited predominantly by bees, with a wide range of smaller insects visiting the flowers less frequently (Table 1).

Average handling times for *E. glabella* and *E. ericoides* were both below seven seconds per flower. *E. abietina*' average handling time was slightly more than double and *E. plukenetii* was almost six times more (Table 1).

3.2 Flower traits

Floral morphometrics of *E. plukenetii* and *E. abietina* were similar to each other but different to the similarities seen between *E. ericoides* and *E. glabella*. Total flowers per plant on both *E. plukenetii* and *E. abietina* rarely reached 100 flowers. Whereas *E. ericoides* and *E. glabella* have a magnitude more flowers per plant (Table 2). One individual of *E. glabella* had 39000 flowers and another of 18000 flowers (both estimated), this is represented in the large standard deviation (SD) seen (Table 2). *E. plukenetii* has the longest corolla tube and the widest corolla opening of the four study species, with *E. abietina* similar, but slightly shorter and narrower. *E. ericoides* and *E. glabella* have similar corolla lengths but *E. ericoides*' opening is slightly wider (Table 2). Nested ANOVA tests between the predicted syndromes revealed insect visited plants had significantly higher total flowers but significantly narrower openings and smaller corolla tubes ($p < 0.001$) (Fig. 4). T-tests between *E. glabella* and *E. ericoides* and also between *E. plukenetii* and *E. abietina* revealed non-significant results ($p > 0.05$) for total flower number, and highly significant differences ($p < 0.001$) for both corolla length and opening within both groups (Table 2).

The white colour of the corolla of *E. ericoides* to the human eye is due to their consistent reflectance of light at wavelengths greater than 400 nm (Fig. 2). The pink-purple/red colour of the other three study species to the human eye is due to their increased reflectance of light between 450 to 600nm (Fig. 2). Reflectance drops sharply at 400 nm and almost all ultraviolet light is absorbed (Fig. 2). Both *E.*

ericoides and *E. glabella* absorb more ultraviolet light than *E. abietina* and *E. plukenetii* (Fig. 2).

3.3 Visitation rates

Normality was achieved through an arcsine of the square root of the proportion of total flowers visited, before an one-way factorial ANOVA test revealed significant differences between the species and a Tukey HSD test revealed no significant differences ($p > 0.05$) between *E. ericoides* and *E. abietina*, with over 80% of the anther rings disturbed in both species (Fig. 3). *E. plukenetii* was significantly lower than both these species ($p < 0.001$), and *E. glabella* was significantly lower than *E. plukenetii* ($p < 0.001$) (Fig. 2).

4. Discussion:

The observations reported are in line with Rebelo et al.' (1985) predictions. *E. glabella* and *E. ericoides* are both potentially pollinated by bees, and *E. plukenetii* and *E. abietina* are potentially pollinated by the orange-breasted sunbird. This can be attributed to their floral morphology (Fig. 4), where the corollas length encourages a mechanism for only similarly sized visitors to break the anther ring upon entry (Johnson et al., 2010), the number of flowers provided for each guild of pollinators is also appropriate as the smaller the desired visitor, the smaller the flower, therefore a larger number of flowers is needed to stand out from the background (Faegri and

van der Pijl, 1966), and the size of the corolla narrowest opening must restrict the entry of undesired, larger visitors (Rebelo et al, 1985).

Floral traits that unlikely to be the main determining factor selecting the pollination system for these *Erica* species (Rebelo et al., 1985) was the reflectance of the visual light spectrum of the corolla. The difference in colour of *E. ericoides* to the other three pink/purple/red ericas does not correlate with the observed potential pollinators (Rebelo and Siegfried, 1985; Kevan, 1978). However it is interesting to note that the two insect pollinated ericas absorbed more ultra violet light than the bird pollinated ericas (Fig. 2). UV rays are highly visible to insects but are no more important in attraction than other wavebands of light reflected from flowers (Kevan, 1978). This explains the bees' visitation of *E. plukenetii*, and the wasps visiting *E. abietina*, despite the lack of UV rays, as there must still be a reward available.

Direct observations of the four study species resulted in some interesting insights. Bees were declined as a potential pollination vector for *E. plukenetii*. Even though visits were frequent, a hole was cut at the base of the corolla tube rather than entering through the corolla opening, by-passing the anthers. Ants and beetles were also seen, but not frequently, and walked around apparently directionless or were motionless. In *E. abietina* the sunbird had a definite method for pollination to occur, where-as the small wasp remains in doubt whether it aids in pollination. However the frequency of the small wasps and their directional tendencies made it obvious that it was entering the flowers for a reward. I could not imagine the wasp breaking

the anther ring, but I could imagine it picking up remnant pollen from the already disturbed anthers. It should be noted that bees were the most common potential pollinators at the study site, which is in line with McCall and Primacks report from 1992. Analyses of pollen loads from bees visiting *E. plukenetii* and wasps visiting *E. abietina* might reveal whether these are potential pollinators of these plants, but it should be noted that pollen morphology of ericas are fairly uniform and identification is almost impossible to Genus let alone species level (Rebelo et al., 1985).

The most powerful conclusions of this preliminary study into in-situ observations of the pollination biology of ericas originates from comparing floral traits to visitation rates. Visitation rates were higher among *E. ericoides* and *E. abietina* (Fig. 3) than the other two *Erica* species, which could imply that *E. ericoides* and *E. abietina* are the preferred species for each pollination system (sunbirds preferring *E. abietina* over *E. plukenetii*, and bees preferring *E. ericoides* over *E. glabella*). Either scent or nectar composition could be important factors in this potential favouritism as this study did not incorporate these variables. However, from this papers' observation, either the spectral composition (Fig. 2) or wider corolla opening (Table 2) of *E. ericoides* could be responsible for the observed favouritism of the bees (both significantly differing from *E. glabella*). This is in contrast to McCall and Primack (1992) where they found that bees made a larger proportion of their visits to pink-red flowers than to white flowers. *E. abietina* could be favoured based on its shortened handling time (Table 1), increasing the sunbirds' foraging efficiency (Levin, 1978), possibly owed to its

shorter corolla tube. This would imply competition for pollinators of two co-residing, co-flowering ericas from two different floral systems within the same habitat.

Little is known about how the CFRs many superficially similar species of *Erica* coexist and apparently avoid hybridizing with each other, but pollination processes are presumably important in this regard (Johnson, 1996; Goldblatt, 1978). Here we have seen how two species of bee visited ericas, and two species of orange-breasted sunbird visited ericas are able to co-exist with similar flowering seasons and the same pollinator despite varying traits presumably affecting pollinator choice.

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Erica plate:

E. ericoides - <http://www.flickr.com/photos/marland/page6/>

E. glabella subsp. *glabella* - <http://za.ispot.org.uk/node/130030>

E. plukenetii - <http://za.ispot.org.uk/node/129973>

E. abietina subsp. *atrorosea* -

http://www.plantzafrica.com/plantefq/ericabiet_atrorosea.htm

Figure legends, Tables and Figures:

Figure 1. Inflorescences of (a) *Erica glabella* subsp. *glabella*, (b) *Erica ericoides*, (c) *Erica plukenetii*, (d) *Erica abietina* subsp. *atrorosea*.

Figure 2. Spectral reflectance of the corollas of the four *Erica* species included in the study. Error bars represent SD around the mean.

Figure 3. Box and whisker plot showing proportion of flowers (arcsine square root of the proportions for normality) visited for all four study species. Significant differences represented by letters ($p < 0.001$). Median, 2nd and 3rd quartiles and non-outlier ranges represented by small box, larger box and error bars respectively.

Figure 4. Mean plot of multiple variables (logged total flowers per plant, corolla length (mm), corolla narrowest opening (mm)) grouped by pollination syndrome. Paired t-tests indicated by letters and significant differences represented by change in case.

Table 1. Visitor observations showing presence as well as time spent visiting each flower of the four study species. Insects not considered as pollinators were left out of consideration.

	Handling time (s) of floral visitors		
	Bird	Large Hymenoptera	Small Hymenoptera
<i>E. glabella</i>		6.30 ± 2.23	
<i>E. ericoides</i>		6.53 ± 2.82	
<i>E. plukenetii</i>	34.00 ± 0.00		
<i>E. abietina</i>	15.12 ± 4.57		30.75 ± 4.60

Table 2. Morphological characters (±SD) of flowering plants of the four study species (n=20). Letters represent significant differences ($p < 0.05$ for total flowers per plant and $p < 0.001$ for corolla length and corolla opening) within columns.

	Flowers per plant	corolla length (mm)	corolla opening (mm)
<i>E. glabella</i>	4365 ± 8946a	3.14 ± 0.20a	1.40 ± 0.12a
<i>E. ericoides</i>	1048 ± 273a	2.97 ± 0.11a	2.17 ± 0.15b
<i>E. plukenetii</i>	77 ± 22b	26.85 ± 0.76b	6.64 ± 0.30c
<i>E. abietina</i>	92 ± 33c	19.98 ± 0.49c	5.02 ± 0.18d

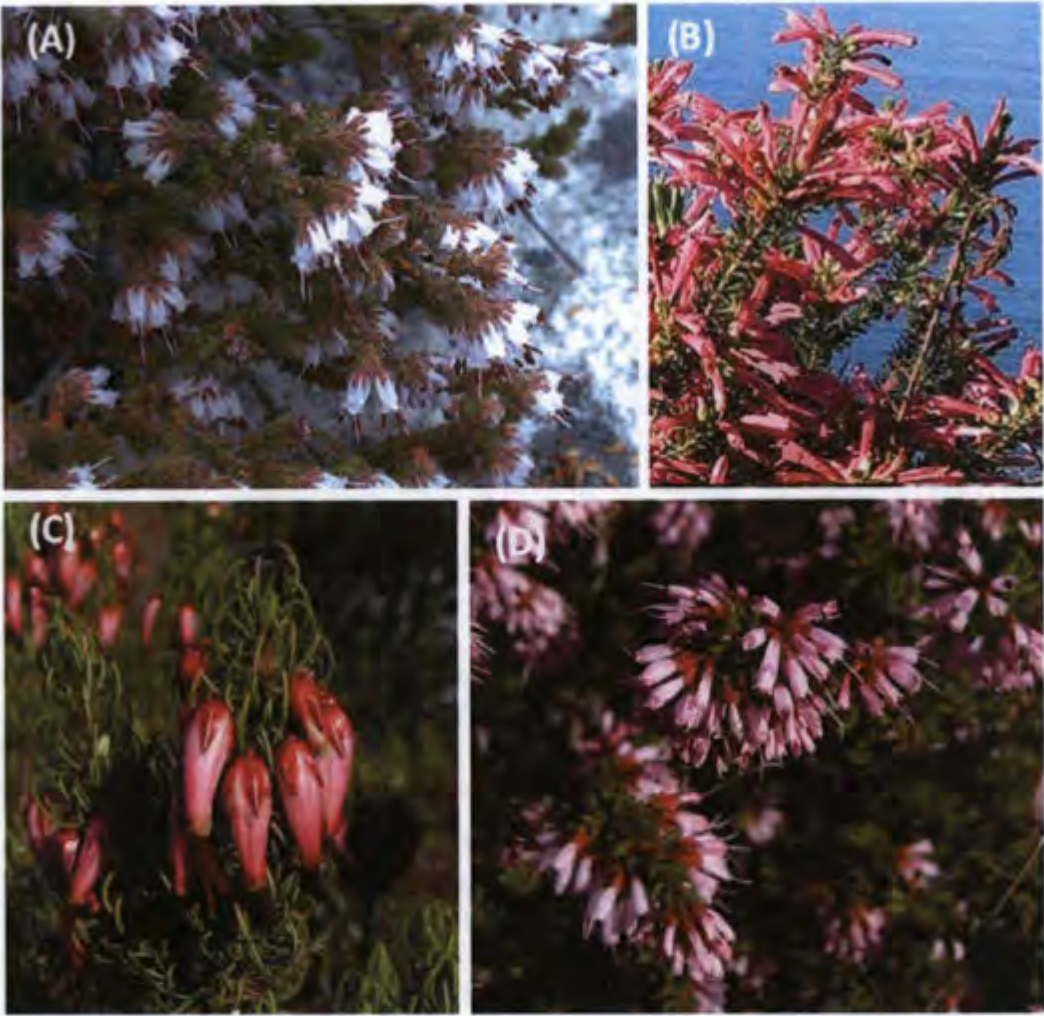


Figure 1.

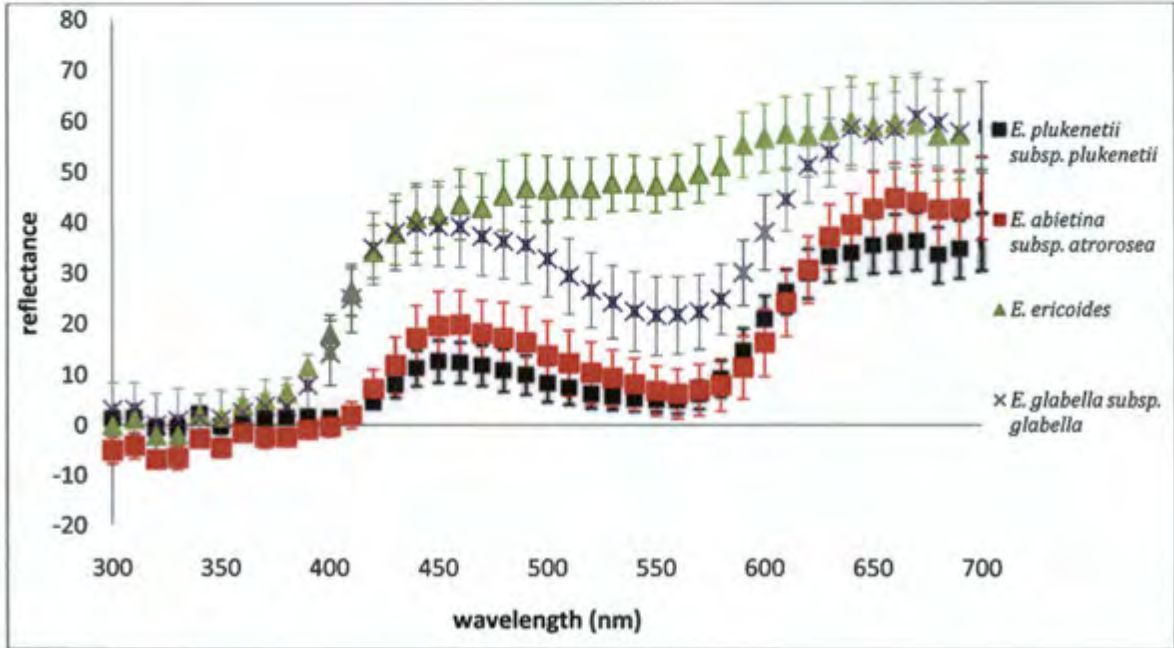


Figure 2.

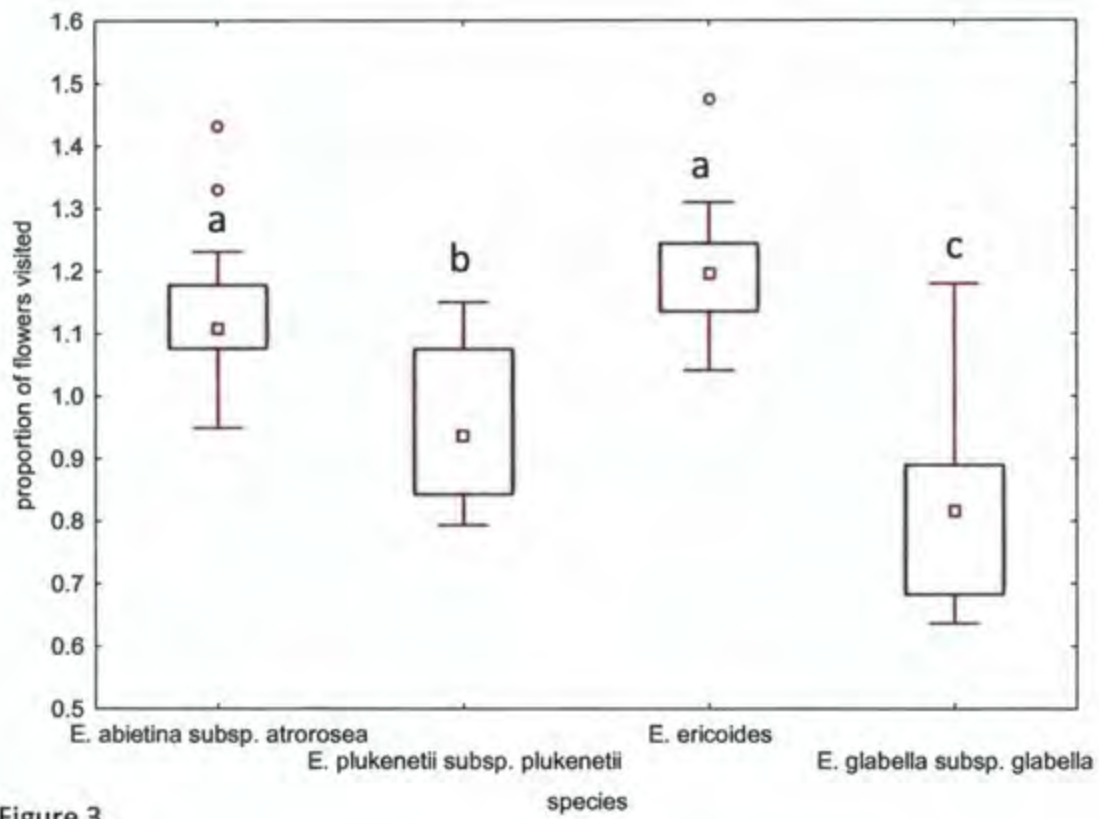


Figure 3.

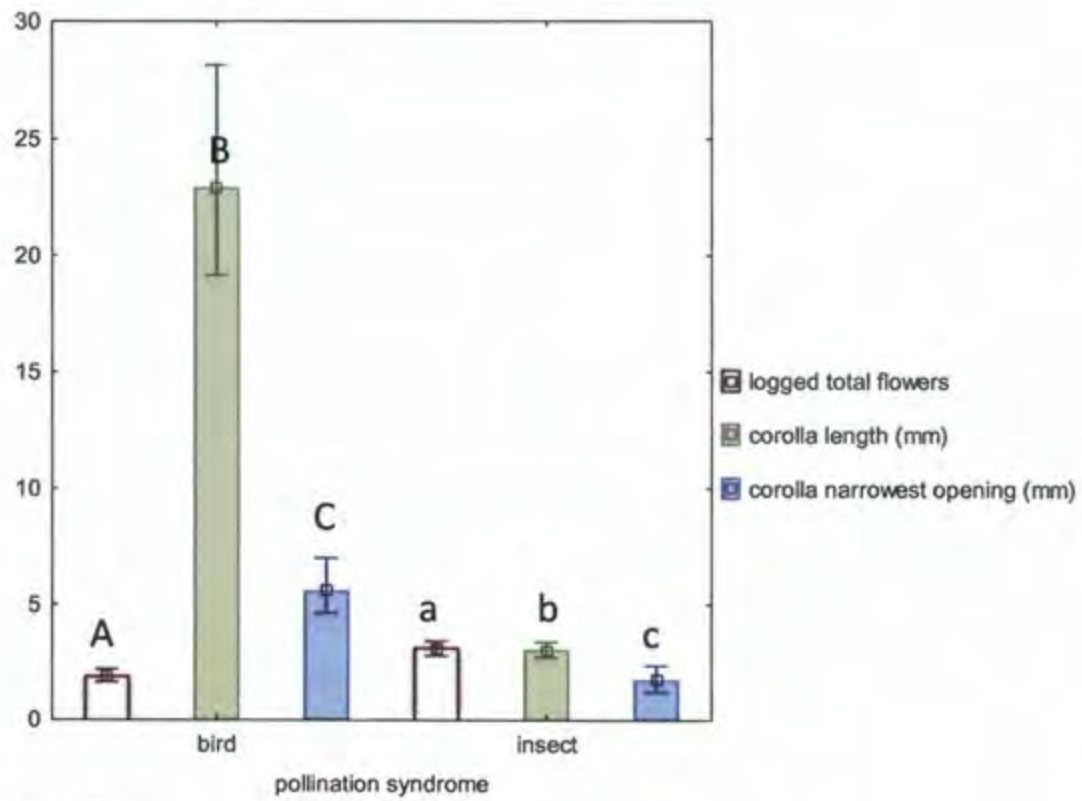


Figure 4.