

1 Do visual traits honestly signal floral rewards at community level?

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26 **AUTHOR'S CONTRIBUTIONS**

27 PLO and MA planned and designed the research. All authors collected the samples and
28 PLO, PFD and DP measured floral traits; ME, MA, PFD and PLO analyzed the data. MA,
29 PLO and ME wrote the first versions of the manuscript that was later edited by all authors.

32 DATA AVAILABILITY STATEMENT

33 Data deposited in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.pg4f4qrn4>,

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1 Do visual traits honestly signal floral rewards at community level?

2 3 4 Abstract

5 1. The high variability observed in floral traits has been interpreted as resulting from the
6 adaptation of plants to pollinators, as the latter present innate preferences for specific floral
7 traits and impose selection over them. However, some pollinators such as bees can learn to
8 associate floral signals with rewards, thus increasing floral constancy on more rewarding
9 flowers. The integration of all these rewards and cues is markedly important at community
10 level, where co-flowering species compete for pollinators.

11 2. In order to verify the honesty of the above mentioned signals, we examined the association
12 between floral visual signals (size, colour, symmetry and floral display) and rewards (pollen
13 and nectar) for 98 species in a Mediterranean community. The associations between floral
14 traits were analysed considering the phylogenetic relationship between the different species.

15 3. Flower colour, size, pollen volume, or amount of sucrose exhibited no phylogenetic signal,
16 which suggests an adaptive evolution in response to different conditions in the pollinator
17 community. Flower size was seen to constitute the most honest signal for pollinators, as this
18 was significantly associated with quantities of pollen and nectar. In contrast, nectar
19 concentration was observed to be positively associated with chromatic contrast. We detected
20 no relationship between flower shape and rewards, on the one hand, or between flower
21 display and rewards, on the other.

22 4. Our study unequivocally demonstrates the correlation between rewards and the visual
23 signals perceived by bees, the most effective pollinators in the Mediterranean Basin. In the
24 community studied, bees employed flower size at longer distances and chromatic contrast at
25 shorter distances to predict rewards. The limited number of studies existing in this sense
26 indicates that this kind of association appears to be community specific.

27 KEY-WORDS: Flower colour, Flower size, Flower symmetry, Mediterranean, Nectar,
28 Plant-pollinator interaction, Phylogenetic signal

29

30 1. INTRODUCTION

31 The process of natural selection has shaped the evolution of zoophilous flowers by matching
32 floral traits with pollinators (Feinsinger, 1983; Stebbins, 1970). The high degree of
33 variability in floral traits, such as colour, scent, size and shape, has been interpreted as the
34 outcome of the selection imposed by pollinators. It has been suggested that unrelated plants
35 adapted to the same functional group of pollinators exhibit floral convergence (traditional
36 pollination syndrome concept, Faegri & van der Pijl, 1979). Nonetheless, the pollinator
37 assemblage visiting a given plant species is often diverse, varying both spatially and
38 temporarily (Herrera, 1996; Waser, Chittka, Price, Williams, & Ollerton, 1996). Regardless
39 of the degree of generalization in a pollination system, plant-pollinator interactions are
40 mostly mediated by the rewards offered by flowers and advertised by means of visual or
41 olfactory signals.

42 Nectar and pollen are the principal rewards offered to pollinators. Nectar plays a key role in
43 plant reproduction by rewarding floral visitors (Simpson & Neff, 1983) and its
44 characteristics, such as concentration, volume, viscosity and chemical composition, can
45 determine plant-pollinator relationships (Baker & Baker, 1983; Heinrich & Raven, 1972;
46 Heyneman, 1983; Kingsolver & Daniel, 1983; Parachnowitsch, Manson, & Sletvold, 2019).
47 Many studies reveal that pollinators (mainly bees) preferentially visit flowers proffering a
48 greater nectar volume or a higher sugar concentration, which they associate with specific
49 floral traits (e.g. Gómez & Perfectti, 2010; Grüter & Ratnieks, 2011). Most experimental
50 studies focus upon nectar because it strongly attracts most pollinators and the nectar
51 parameter is easily manipulated for research. Pollen is an important protein source, providing

52 the greater part of the dietary nitrogen required by most bees and many other insects, and by
53 bats (Law, 1992) or birds (Grant, 1996). Pollen is particularly important for bees, as it
54 represents the main protein source for their larvae. Bees show preferences for pollen sources
55 with a higher protein:lipid ratio (Ruedenauer, Spaethe, van der Kooi, & Leonhardt, 2019;
56 Vaudo, Patch, Mortensen, Tooker, & Grozinger, 2016). However, despite the importance of
57 pollen for bees, the main pollinators in the majority of natural communities, few studies
58 focus on pollen as a reward (Muth, Papaj, & Leonard, 2016; Nicholls & Hempel de Ibarra,
59 2014, 2017).

60 Floral designs likely evolved to advertise concealed or access-limited rewards; thus, floral
61 traits such as colour, size or shape would appear to act as signals enabling plants to announce
62 their rewards (Fenster, Cheely, Dudash, & Reynolds, 2006). For a signal to be reliable for
63 pollinators, it must be honest, i.e. it must be correlated with the quantity or quality of the
64 reward (Armbruster, Antonsen, & Pélabon, 2005; Knauer & Schiestl, 2015). In certain
65 circumstances, there can be a disassociation between floral signal and reward; for example,
66 when a visitor has foraged upon a flower, its nectar can be temporally depleted, and the floral
67 signal therefore becomes dishonest for some time. Accordingly, some pollinators such as
68 honeybees and bumblebees deposit short-lived repellent scents to communicate reward
69 depletion to congeners (Stout & Goulson, 2001); however, many others are unable to do this.
70 In addition, pollinated or old flowers usually stop secreting nectar and their signals can
71 become dishonest if the corolla remains intact for some time. Despite these temporary
72 mismatches between floral signals and rewards, plants providing a more abundant reward
73 will generally possess higher nectar standing crops and/or larger amounts of available pollen
74 (Cohen & Shmida, 1993; Jachuła, Wrzesień, Strzałkowska-Abramek, & Denisow, 2018);
75 this would generally render their distinctive signals honest and would enable pollinators to
76 remember them as providing a reward (Knauer & Schiestl, 2015; McLinn & Stephens, 2006).

77 Notwithstanding, some plant species produce little or no rewards, and can benefit from
78 pollinator visits by mimicking the signals of the rewarding plants existing in a community
79 (Schiestl & Johnson, 2013; Vereecken & Schiestl, 2008). However, their mimicry can be
80 considered to be adaptive only if this similarity with regard to signals enhances plant fitness
81 (Roy & Widmer, 1999).

82 Pollinators can show both perceptual bias and innate preference for some floral traits, and
83 they tend to visit these flowers more frequently (Chittka & Raine, 2006; Gómez et al., 2008;
84 Grüter, Moore, Firmin, Helanterä, & Ratnieks, 2011; Gumbert, 2000; K. Lunau & Maier,
85 1995; Rohde, Papiorek, & Lunau, 2013; Schiestl & Johnson, 2013). However, some of the
86 principal pollinators can learn and memorize associations between some floral traits and
87 rewards, thus overriding their innate preferences (Chittka & Raine, 2006; Gómez et al.,
88 2008; Grüter & Ratnieks, 2011; Gumbert, 2000; Lunau & Maier, 1995; Rohde et al., 2013).

89 Specifically, bees exhibit a high learning capacity, responding rapidly to an artificially
90 increased reward (e.g. Morse, 1980; Nicholls & Hempel de Ibarra, 2014; Schaffer & Schaffer,
91 1979; Thomson, 1988; Waddington et al., 1981) by increasing floral constancy (Grüter et
92 al., 2011). Thus, foraging pollinators use floral traits as predictors of rewards (Chittka, Dyer,
93 Bock, & Dornhaus, 2003; Giurfa, 2004; Makino & Sakai, 2007). In any case, flower choice
94 by pollinators constitutes a complex mechanism possibly involving many factors, both
95 intrinsic, such as perceptual abilities or innate preferences (Lunau & Maier, 1995; Schiestl
96 & Johnson, 2013), and extrinsic ones, like alternative flower resources or competitors
97 (Inouye, 1978; Lázaro, Lundgren, & Totland, 2009; Mitchell, Flanagan, Brown, Waser, &
98 Karron, 2009).

99 In seasonal communities, which present a high degree of flowering overlap, many plants
100 may compete simultaneously for pollinator services (Herrera, 1988; Petanidou, Ellis,
101 Margaris, & Vokou, 1995). In such a situation, rewarding plant species could be expected to

102 produce distinctive signals that can be memorized by pollinators, consequently promoting
103 their floral constancy (Schiestl & Johnson, 2013), which would result in enhanced plant
104 fitness due to an increase in intraspecific pollen receipt and export, and a decrease in
105 heterospecific pollen deposition (Feinsinger, 1987; Wright & Schiestl, 2009). At plant
106 community level, pollinators' choice of flowers may generate differences in reproductive
107 success among plant species, affecting their population dynamics (Levin & Anderson, 1970;
108 Morales & Traveset, 2009). In turn, pollinators that make correct foraging decisions will be
109 more efficient with regard to acquiring nutrients and increasing their foraging efficiency,
110 thus enhancing fitness levels (Burns & Dyer, 2008; Chittka et al., 2003; Dyer et al., 2012).
111 Briefly, many evolutionary processes are involved in adjusting flowers' reward signalling to
112 pollinators' foraging choices (Balamurali, Krishna, & Somanathan, 2015; Schiestl &
113 Johnson, 2013), but assessing these factors falls outside the scope of our study. The present
114 paper attempts to verify the existence of phenotypic associations between floral visual
115 signals and rewards (pollen and nectar) at community level in the Mediterranean Basin in
116 order to assess the honesty of the signals. The association between rewards and floral cues
117 mediates pollinator services at community level (Herrera, 2020). However, there has been
118 scant research on this relationship at the aforementioned level (Chittka, Ings, & Raine, 2004;
119 Kantsa et al., 2017; Shrestha, Garcia, Burd, & Dyer, 2020) and the offer both of nectar and
120 of pollen has never been studied. In the Mediterranean Basin, most species flower in the
121 spring, coinciding with maximum richness of insect taxa (Herrera, 1988). We focused on the
122 sensory capacities of bees because i) they are the main pollinators in the Mediterranean Basin
123 (Petanidou & Ellis, 1993; Potts et al., 2006), which is one of the world's centres of bee
124 speciation (Michener, 2000), ii) they depend on pollen and nectar for survival and
125 reproduction, iii) they depend on pollen more than any other group of pollinators in the
126 Mediterranean (Petanidou & Ellis, 1993) and iiiii) there has been abundant research on their

127 sensory capacities for floral trait discrimination (e.g. Chittka & Wells, 2004; Garcia et al.,
128 2017). We recorded the floral rewards and flower traits of 98 melitophilous species in a
129 Mediterranean community. To avoid the phylogenetic bias in flower traits and reward
130 association resulting from species composition, we tested the degree of association
131 controlling the non-independence of the species using a phylogeny of the community. The
132 possible association between rewards and floral visual signals, on one hand, and the
133 associative learning by bees in a community context, on the other, can play an important role
134 in the evolution of flower variability in the Mediterranean Basin, one of the world's
135 biodiversity hotspots (Médail & Quezel, 1997).

136

137 2. MATERIAL AND METHODS

138 2.1. Study site

139 The relationship between flower colour and rewards was studied along the year in a species-
140 rich natural Mediterranean community situated in the Natural Park of Doñana (37° 15' – 37°
141 20' N and 6° 30' – 6° 32' W). The community consists of assorted scrubland and rich
142 grasslands, with scattered-to-dense woodland, mainly containing *Quercus suber* and *Pinus*
143 *pinea*. The shrub layer mainly comprises species of Cistaceae, Lamiaceae, Fabaceae or
144 Rosaceae. The grasslands, much more diverse, mostly consist of species of Liliaceae,
145 Ranunculaceae, Plantaginaceae, Lamiaceae, Brassicaceae, Fabaceae, Caryophyllaceae or
146 Asteraceae. We sampled a total of 98 native species from 33 families, including trees, shrubs
147 and herbs. These species were selected because they are visited by bees, whereas other
148 flowering species of the community, pollinated by ants (De Vega, Arista, Ortiz, Herrera, &
149 Talavera, 2009) or dipterans (Berjano, Ortiz, Arista, & Talavera, 2009), were not sampled.

150

151 2.2. Floral visual signals

152 We recorded symmetry, size and colour of flowers for each species studied; we also recorded
153 floral display size for a subset of these species on a scale ranging from low to high (n = 42).
154 We considered two categories of flower symmetry: “bilateral” for flowers with a single plane
155 of symmetry and “radial” for flowers exhibiting more than one plane. To characterize flower
156 size, we considered the diameter for radial flowers, whereas for bilateral flowers we
157 contemplate the longest axis of flower silhouette as perceived by pollinators on approaching
158 the flowers. These measurements were provided by the *Flora Vascular de Andalucía*
159 *Occidental* by Valdés et al. (1987b), considering for each species the middle value of the
160 range shown in the latter Flora. For the Asteraceae species, we considered head size, rather
161 than flower diameter, because in the plants of this family, the head constitutes the visual unit.
162 For each species, we measured the colour of three recently opened flowers from different
163 plants. We obtained spectral reflection functions of the adaxial surface of the petals of each
164 flower at wavelengths from 300 to 700 nm by using an Ocean Optics reflectance
165 spectrometer as well as Spectra Suite software. Our spectrometer device incorporated a
166 probe with a deuterium-tungsten halogen light source (200-2,000 nm) and a black metal
167 probe-holder with a 6mm-diameter opening at a 45° angle, in which the probe was always
168 fully inserted. We used a UV-reflecting white standard provided by the same manufacturer
169 to calibrate the spectrometer. We glued each petal sample as flat as possible on the sticky
170 side of a piece of black electrical insulation tape, attaching it to the basal opening of the
171 probe-holder to prevent any external light from interfering. We first used procspec function
172 in the R package PAVO to zero any negative value in the spectral functions obtained (Maia,
173 Gruson, Endler, & White, 2019). We then averaged the spectral reflection functions for each
174 species and for noise removal, we once again employed the procspec function of the R
175 package PAVO to smooth each averaged spectral function (Maia et al., 2019). For each
176 species we selected the wavelength range to be smoothed, as well as the appropriate

177 smoothing span in order to avoid any break point in the resulting smoothed functions. To
178 assess petal colours as perceived by bees, we plotted the smoothed spectral function of each
179 species in the colour hexagon diagram, which is a model of bee colour space that enables
180 colours to be categorised and contrasts among these as seen by bees to be assessed (Chittka,
181 1992; Chittka, Shmida, Troje, & Menzel, 1994). Accordingly, we assigned each species to
182 one of the six recognised bee colour categories (UV, UV-Blue, Blue, Blue-Green, Green and
183 UV-Green; Chittka et al., 1994) and we calculated its distance to background in hexagon
184 units (hereafter chromatic contrast; Chittka & Kevan, 2005; Spaethe, Tautz, & Chittka,
185 2001). In addition, also based on the bee vision model, for each species we calculated the
186 excitation generated in the green photoreceptor after adaptation to the background (hereafter
187 green contrast; Ng, Garcia, & Dyer, 2018; Spaethe, et al., 2001), as well as the sum of
188 excitations generated in the blue, green and UV photoreceptors following adaptation to the
189 background (hereafter brightness contrast; Ng et al., 2018; Spaethe et al., 2001). Using the
190 smoothed spectral function of each species, we also calculated reflectance amplitude and
191 spectral purity. Reflectance amplitude, i.e. the averaged reflectance at all wavelengths,
192 represents the area under the reflectance curve and refers to the intensity of a stimulus (Grill
193 & Rush, 2000; van der Kooi, Dyer, Kevan, & Lunau, 2019). Spectral purity is the difference
194 between the maximum and minimum values of reflectance divided by the mean value of
195 reflectance; it is indicative of colour saturation (Koethe, Bossems, Dyer, & Lunau, 2016;
196 Valido, Schaefer, & Jordano, 2011). All these parameters might be used as discriminative
197 visual cues for bees (Bukovac et al., 2017; Cazetta, Schaefer, & Galetti, 2009; Dyer,
198 Streinzer, & Garcia, 2016; Lunau, Konzmann, Winter, Kamphausen, & Ren, 2017; Spaethe
199 et al., 2001; van der Kooi et al., 2019).

200 To assess floral display size, we estimated the number of flowers at anthesis in 10-12 plants
201 of each species once a week along the whole flowering period; the maximum number of

202 flowers at anthesis recorded for each individual was used as an estimate of its floral display
203 size; subsequently we obtained an average for each species.

204

205 2.3. Floral rewards

206 Data on floral reward production for most species in the community were obtained from two
207 different sources: i) we made use of the data included in two earlier extensive studies on
208 nectar and pollen production in the same community (Ortiz, 1991; Talavera, Herrera, Arroyo,
209 Devesa, & Ortiz, 1988) and ii) for species not included in the latter studies, we assessed
210 nectar and pollen production following the same procedures employed therein in such a way
211 that both datasets were comparable. Specifically, we assessed nectar production in one-three
212 flowers of ten plants after being bagged for 24 hours, quantifying nectar volume with
213 microcapillary tubes and measuring nectar concentration (°Brix) with a manual
214 refractometer, and then calculating sugar mass per flower (sucrose equivalent weight;
215 Cruden & Hermann, 1983). To assess pollen reward we used both pollen number and pollen
216 volume (Buchmann & O’rourke, 1991; Müller et al., 2006; Potts et al., 2003). We first
217 estimated the mean number of pollen grains produced per flower by counting the pollen
218 grains of five-ten flower buds from different plants of each species. Prior to pollen counting,
219 we dissected floral buds under a stereomicroscope to ensure that anthers remained unopened
220 and presented no sign of predation. Pollen volume constitutes a useful trait for assessing bee
221 diet (Buchmann & O’rourke, 1991); we therefore estimated the mean volume of pollen
222 offered by flowers of each species as the product of the mean number of pollen grains per
223 flower and the volume of an individual pollen grain. To calculate individual pollen grain
224 volume, we considered each grain as an ellipsoid, considering the lengths of the polar and
225 equatorial axes as in Valdés et al. (1987a).

226

227 2.4. Phylogeny

228 We obtained a phylogenetic tree of the 98 species included in the present study using the
229 function phylo.maker implemented in the R package V.PhyloMaker (Jin & Qian, 2019).
230 Species names and the taxonomic framework (genera and families) were edited to fit with
231 the ones used by v.phylomaker (which are based on The Plant List (TPL, ver. 1.1;
232 www.theplantlist.org). We established the options: tree = GBOTB.extended, nodes =
233 nodes.info.1 (the genus- or family-level largest cluster's root and basal node information was
234 extracted from the mega-tree) and scenarios = "S3" (new species tips are binded to genus-
235 or family-level following specific rules, see Jin & Qian, 2019 for more details). The mega-
236 tree GBOTB.extended is a corrected combination of GBOTB for seed plants (Smith &
237 Brown, 2018) and Zanne et al.'s (2014) phylogeny for pteridophytes. GBOTB.extended
238 includes 479 families, 10,587 genera and 74,533 species of vascular plants. The alternative
239 options nodes = nodes.info2 (the genus- or family-level root and basal nodes information
240 was extracted from a phylogeny, regardless of whether the genus or family is monophyletic
241 in the mega-tree) and scenarios = "S1" (new species tips are binded to the genus- or family-
242 level basal node) or "S2" (new tips are binded to a randomly selected node at and below the
243 genus- or family-level basal node) were also explored, but the resulting trees were very
244 similar (see more details referring to the possible options for building the trees in Jin & Qian,
245 2019).

246

247 2.5. Statistical analysis

248 To assess the importance of floral visual signals (colour, size, symmetry, and display size)
249 in accounting for reward (nectar or pollen), rewards were regressed against flower characters.
250 The response variables for these linear regressions were the reward parameters (different
251 measures of pollen or nectar production). The predictors for those regressions were flower

252 colour parameters, flower size, flower symmetry and floral display size. To assess the
253 possible relationship between visual signals, we performed linear regression analyses with
254 flower size, flower symmetry and floral display size as response variables, and flower colour
255 parameters as predictor variables. Additionally, we performed linear regression analyses
256 between nectar parameters as response variables and pollen parameters as predictors. To
257 correct for the non-independence of species traits resulting from genealogical relationships
258 between species, these regressions were performed with the use of phylogenetic generalized
259 least squares analyses as implemented in the `pgls` function from R the package `caper` (Orme
260 et al., 2013, R Development Team 2019). We set λ as a free parameter to be estimated.
261 The phylogenetic signal of all regressions and variables was estimated using λ as
262 implemented in the `pgls` function. We did not assume a phylogenetic signal (a pure Brownian
263 Motion model); rather, we used the estimated λ to transform the branch length of the
264 phylogeny and the resulting variance-covariance matrix in our regression analyses (Pagel,
265 1999). The phylogenetic signal of the categorical variables was calculated with the function
266 `fitDiscrete` from the R package `geiger` (Harmon, Weir, Brock, Glor, & Challenger, 2008) for
267 multiple state traits. The continuous variables were plotted on the phylogeny with the
268 function `contMap` from the R package `phytools` (Revell, 2012). To correct significance for
269 multiple testing, significance levels were adjusted by means of the Bonferroni correction.
270 However, due to the conservative nature of Bonferroni, we have reported all the results
271 including exact p-values whilst indicating significances after Bonferroni corrections (Moran,
272 2003).

273 In addition, to ascertain the importance of the measured visual signals in predicting pollen
274 and nectar rewards, we conducted multivariate phylogenetic analyses. The predictors for
275 these regressions were flower colour parameters, flower size, and floral display size. Since
276 floral display size was measured in a subsample of 42 species, we performed two sets of

277 analysis, one on these 42 species taking into consideration all the visual traits as predictors,
278 and the other on the 98 species without taking “floral display size” into consideration. The
279 multivariate phylogenetic analyses were performed establishing the same options as in the
280 univariate phylogenetic analyses (see before). Lastly, given that one species, *Cistus ladanifer*,
281 provided extreme values for rewards and flower size, to avoid bias resulting from one single
282 species, we also ran multivariate phylogenetic analyses without considering this species, and
283 similar significant associations were observed (see Table S1 in Supporting Information).

284

285

286 3. RESULTS

287 3.1. Trait Variability

288 The plant community displayed a high degree of variability in all the traits measured (Table
289 1). Dataset is available in Dryad Data Repository (doi:10.5061/dryad.pg4f4qrn4; Ortiz,
290 Fernández-Díaz, Pareja, Escudero, & Arista, 2020). Approximately 60% of the species
291 possessed radial flowers and 40 % bilateral flowers, the latter species being mainly Fabaceae
292 and Lamiaceae. Mean flower size was 18.26 ± 1.4 cm (Table 1) and ranged from 1.5 to 45
293 mm for most species, but the flowers of *Cistus ladanifer* were markedly bigger (95 mm) than
294 the remaining ones. Floral display size also showed a high level of variability, with a mean
295 of 1043 ± 371 flowers and ranging from only one flower (*Papaver rhoeas*) to over 12000
296 flowers (*Retama sphaerocarpa*). As for the bee colour categories in the hexagon model, most
297 of the species were situated in the Blue or the Blue-Green sectors, the UV flowers being the
298 least common ones (Fig. 1a). As perceived by humans, white and yellow flowers were by
299 far the most frequent (33% and 25% respectively), and these human-yellow flowers were
300 classified into four different bee-colour categories (Fig. 1a). In contrast, human-red or
301 human-orange flowers were very scarce and corresponded exclusively to the UV bee-colour

302 category. Only 38% of the species had UV-reflecting flowers (either UV, UV-Blue, or UV-
303 Green), and almost half of these were human-yellow flowers (Fig. 1a and 1b).

304

305 The offer of floral rewards varied greatly among species. The flowers of almost one third of
306 the species in the community (33%) were nectarless; these species belonged to as many as
307 13 different families, Fabaceae being the most frequent (11 species). For the remaining
308 species (67%), nectar-secreting flowers were found, their mean nectar concentration being
309 nearly 29°Brix; *Cistus* species exhibited extremely high concentrations, even over 100°Brix
310 (*C. salvifolius* and *C. monspeliensis*) due to sugar crystallization, thus contributing to the
311 high mean community value (Table 1). Sugar mass and pollen volume showed the highest
312 coefficients of variation (Table 1). Most nectar-secreting flowers produced less than 200 µg
313 of sugar per day and only those of seven species produced more than 1mg; the flowers of
314 *Erophaca baetica* (Fabaceae) were the most nectar-rewarding (3 mg). Likewise, the flowers
315 of most species offered less than 0.5 mm³ of pollen, but those of *Papaver rhoeas* and *Cistus*
316 *ladanifer* offered 13 and 30 mm³, respectively.

317

318 3.2. Phylogenetic signal of floral traits

319 A well-solved phylogeny was constructed for the 98 species studied (Fig. S1). Strong
320 phylogenetic signals were found for some floral visual traits (Fig. 2) but not for others (Fig.
321 S2). Floral symmetry and reflectance amplitude showed the highest λ values, indicating that
322 their variation was mainly explained by the phylogeny (Table 2). The strong phylogenetic
323 signal of reflectance amplitude was due to the high values of flowers of Brassicaceae or
324 Convolvulaceae and the low values in Boraginaceae. The other flower colour parameters
325 and flower size showed no significant high values for λ .

326 Among the reward parameters, variability in pollen grains produced per flower was
327 accounted for mainly by phylogeny ($\lambda = 0.726$). Some families such as Boraginaceae,
328 Rosaceae or Cistaceae presented a high number of pollen grains per flower, while others
329 such as Ericaceae or Convolvulaceae produced a low number. Nectar presence and sugar
330 concentration also showed a strong phylogenetic signal ($\lambda = 0.922$ and $\lambda = 0.878$,
331 respectively) with families such as Cistaceae producing highly concentrated nectar. In
332 contrast, pollen volume and sucrose mass exhibited no significant phylogenetic signals
333 (Table 2 and Fig. S2).

334

335 3.3. Phenotypic association among floral traits

336 Based on the optimal models (fitted lambda), positive and significant associations were
337 observed between sugar mass and pollen grain number, on one hand, and between sugar
338 mass and pollen volume, on the other. We also detected significant associations between the
339 following pairs of visual signals: brightness contrast and floral display size, brightness
340 contrast and symmetry, bee-hexagon categories and floral display size, spectral purity and
341 symmetry, and green contrast and flower size (Table 3). However, these associations were
342 not significant after Bonferroni correction and the remaining associations were also not
343 significant (Table S2).

344

345 Multivariate phylogenetic regressions showed that flower size was the only visual signal
346 significantly associated with both rewards (Table 4). Flower size presented a strong, positive
347 and significant association with pollen number and volume and also with sugar mass (Fig.
348 3; Table 4); this occurred even after removing *Cistus ladanifer*, the species with the largest
349 and most pollen-rewarding flowers, as well as the fourth most nectar-rewarding ones (Table
350 S1). We observed high adjusted r^2 -values for the relationships between flower size and both

351 pollen volume and pollen grains per flower ($r^2 = 0.655$ and 0.388 , respectively; Fig. 3). On
352 the contrary, only chromatic contrast was positively and significantly associated with sugar
353 concentration (Fig. 3, Table 4). Similar results were obtained when multivariate
354 phylogenetic regressions included “floral display” (Table S3), as this trait was not associated
355 with any reward parameter. The only difference was seen to be in the multivariate model for
356 sugar concentration, as all the colour variables and flower size proved to be significantly
357 associated with sugar concentration (Table S3). Despite the big differences in pollen volume
358 and sucrose amount among the colour hexagon categories, these were not significant due to
359 the strong variability within each category (Table S2). Similarly, flower shape (radial or
360 bilateral) showed no significant association with any rewards, although we did detect a
361 tendency in the radial flowers to produce higher pollen volumes.

362

363 4- DISCUSSION

364 Despite the abundant literature on plant-pollinator interactions at community level, little is
365 as yet known about the relationship between floral visual signals and rewards. The wide
366 range of plant species in the present study highlights the association between rewards and
367 certain visual signals that are perceived and learnt by pollinators, specifically by bees.

368

369 4.1. Selection and phylogenetic inertia of floral traits

370 In the community studied, some floral traits presented significant phylogenetic signals,
371 suggesting it is unlikely that pollinators have recently exerted strong selection. Among floral
372 visual cues, symmetry and reflectance amplitude exhibited a strong phylogenetic signal. This
373 phylogenetic signal of reflectance amplitude is surprising, especially because no other colour
374 parameter displayed any phylogenetic inertia. Reflectance amplitude is perceived as the
375 intensity of the stimulus; its role in pollinator attraction is still unclear and some authors

376 even suggest that it is unimportant to bees (Ng, Garcia, & Dyer, 2018; van der Kooi et al.,
377 2019). We encountered no explanation for the phylogenetic inertia detected in this flower
378 colour trait. However, reflectance amplitude depends both upon pigmentary coloration and
379 on petal structure (van der Kooi et al., 2019) and that structure characterizes some clades
380 (e.g. *Ranunculus*, van der Kooi et al., 2017). Differences between clades might possibly be
381 due to differences in petal structure.

382 In contrast, a low phylogenetic signal was found in sugar mass and pollen volume per flower
383 (the most indicative parameters of reward value), most colour parameters, and flower size.
384 These traits showed a high variability at community level, which might suggest an adaptive
385 evolution in response to different conditions in the pollinator community. This hypothesis is
386 supported by the results of a meta-analysis that demonstrated that the degree of dependence
387 of a plant species upon insects for pollination correlated with its pollen nutritional content,
388 regardless of phylogeny (Ruedenauer et al., 2019). The lack of a phylogenetic signal in
389 flower colour when using spectral reflectance measures has previously been reported in other
390 communities (Arnold et al., 2009; McEwen & Vamosi, 2010; Shrestha et al., 2014; but see
391 Reverté et al., 2016). It has been suggested that flower colour constitutes an evolutionarily
392 labile trait, frequently subjected to natural selection; indeed, colour changes are frequent
393 within flowering plant clades (e.g. Beardsley, Yen, & Olmstead, 2003; McEwen & Vamosi,
394 2010; van der Kooi & Stavenga, 2019) or even within species (e.g. Imbert et al., 2014; Irwin
395 & Strauss, 2005; Narbona et al., 2018; Turelli et al., 2001; Zufall & Rausher, 2003). Colour
396 changes commonly occur in populations as a consequence of mutations in the anthocyanin
397 biosynthetic pathway, and their maintenance is usually attributed to selection mediated by
398 pollinators (e.g. Hopkins & Rausher, 2012; Irwin & Strauss 2005; Narbona et al., 2018).

399

400 4.2. Flower size: The most honest signal for pollinators

401 Our extensive sampling of co-occurring species in a Mediterranean community clearly
402 indicates that flower size, rather than flower colour or other visual signals, is the most honest
403 signal to pollinators. Bigger flowers produced a higher pollen volume, pollen grain number
404 and sucrose amount, even after correcting for the phylogenetic dependency of species traits,
405 and following Bonferroni correction. The relationship between flower size and nectar
406 production has frequently been reported (e.g. Herrera, 1985; Petanidou & Smets, 1995,
407 Petanidou et al., 2000), but few studies refer to the association of flower size with pollen
408 grain number or pollen volume (Chouteau, Barabé, & Gibernaut, 2006; Stanton & Preston,
409 1988). Moreover, these associations were relatively strong (adjusted $r^2=0.655$ for pollen
410 volume and $r^2=0.388$ for pollen grain number) and they could therefore be used as honest
411 signals that are easily learnt by bees or other pollinators (Blarer, Keasar, & Shmida, 2002;
412 Grüter & Ratnieks, 2011).

413 Over long distances, flower size is probably the most important visual cue for floral
414 perception (Hempel de Ibarra, Langridge, & Vorobyev, 2015). The association between
415 flower size and rewards suggests that pollinators can reliably assess flower reward quantity
416 from a distance. If, as has been reported (Blarer et al., 2002; Chittka & Raine, 2006; Gómez
417 et al., 2008; Grüter & Ratnieks, 2011; Gumbert, 2000), bees rapidly learn to associate visual
418 signals with the most rewarding flowers, then a higher floral constancy is to be expected on
419 the bigger flowers, which in turn will enhance flower fitness. Indeed, in a previous study in
420 the same community involving the large flowers of *Cistus salvifolius*, an experimental
421 reduction of flower size caused a sharp drop in both male and female fitness as a
422 consequence of fewer pollinator visits (Arista & Ortiz, 2007). Similarly, a recent study in
423 another Mediterranean community also revealed a positive relationship between pollinator
424 visitation rates and flower size (Herrera, 2020), thus indicating the importance of floral size
425 in pollinator attraction.

426 Flower size also showed a significant association with the green-contrast parameter,
427 although only prior to Bonferroni correction. Green-contrast is the contrast between a visual
428 stimulus and its background mediated solely by the green photoreceptor, and many insects
429 use this to detect flowers from large distances (van der Kooi et al., 2019). It has been
430 suggested that plants with small flowers need to compensate for their low level of
431 conspicuousness by increasing this green-contrast in order to better attract bees (van der
432 Kooi et al., 2019). This hypothesis has not been tested previously, and only a study by
433 Hempel de Ibarra & Vorobyev (2009), based on photographed flowers, has provided any
434 evidence to support it. Nonetheless, our research, based on spectral measurements, did not
435 corroborate this theory, even indicating evidence to the contrary, as bigger flowers also
436 displayed a higher degree of green-contrast, thus becoming much more conspicuous, and
437 increasing their visual attractiveness to bees.

438

439 4.3. Flower colour: A trait weakly associated with reward production

440 It has been hypothesised that co-occurring species with overlapping flowering tend to be
441 more divergent in floral colour than might be expected by chance as a way to ensure floral
442 constancy and avoid competition for pollinators (Botes, Johnson, & Cowling, 2008; Caruso,
443 2000; Chittka, Thomson, & Waser, 1999; Dyer & Chittka, 2004; Spaethe et al., 2001; van
444 der Kooi, Pen, Staal, Stavenga, & Elzenga, 2016). The few studies addressing this issue have
445 provided some evidence in this sense (McEwen & Vamosi, 2010; Shrestha et al., 2014). In
446 our community, floral colour showed a high variability, with most species situated at the
447 blue, blue-UV and green-UV sectors of the hexagon, and many of these species were
448 separated by at least 0.2 hexagon units (Euclidean distance; see Fig. 1a), the minimum
449 threshold with regard to enhancing floral constancy by bees (Dyer & Chittka, 2004; Spaethe
450 et al., 2001). Surprisingly, congeneric plants, very similar in flower size, shape, and colour

451 to the human eye, were seen by bees to display different colours, thus indicating that these
452 pollinators can discriminate clearly between them. For example, despite the high similarity
453 in visual cues from a human perspective, *Halimium calycinum* and *Halimium halimifolium*
454 (Cistaceae) were situated at UV and Green-UV hexagon sectors respectively, and, for
455 instance, *Ononis baetica* and *Ononis pinnata* (Fabaceae) were situated at Blue-Green and
456 Blue sectors, respectively. In closely related species, floral differentiation is probably
457 selected as a way to enhance floral constancy, preventing the formation of maladapted
458 hybrids and maintaining species integrity (Levin, 1972); consequently, differences in colour
459 as perceived by bees might have been selected in these similar co-flowering species. Indeed,
460 in the present paper this hypothesis is supported by the generally weak phylogenetic signal
461 found for the colour parameters.

462 Other species in the community studied, albeit different in colour to the human eye, were
463 situated close together in the bee vision model, at below 0.1 hexagon units (Euclidean
464 distance). Although the Chittka model establishes a Euclidean distance of 0.1 hexagon units
465 as the threshold value for colour discrimination by bees (Chittka, 1992; Chittka & Kevan,
466 2005), recent physiological models have reported a higher discrimination capacity by bees,
467 because colour discrimination obeys sigmoidal-shaped functions (Garcia, Shrestha, & Dyer,
468 2018; Garcia et al., 2017). These new models of bee colour discrimination have been
469 supported by both experimental (Garcia et al., 2018) and empirical data (Jiménez-López,
470 Matas, Arista, & Ortiz, 2019). However, the ability of bees to discriminate between flowers
471 presenting very small hexagon distances depends on context (Dyer, 2006; Dyer & Chittka,
472 2004) and it is therefore difficult to ascertain whether bees can discriminate among these
473 species in the community studied.

474 Although flower colour has traditionally been considered to be one of the most important
475 signals in pollinator attraction, in our community it was significantly associated only with

476 the nectar-quality parameter. Chromatic contrast was the most important colour parameter
477 associated with nectar concentration, this association accounting for 7.3% of reward
478 variability. Chromatic contrast has previously been proven to play a significant role at the
479 plant community level (van der Kooi et al., 2019) and it has been suggested that plant species
480 may maximize chromatic contrast as a way to distinguish themselves from their co-flowering
481 neighbours (McEwen & Vamosi, 2010; van der Kooi et al., 2016). Given the importance of
482 chromatic contrast for visual detection by bees (Dyer, Whitney, Arnold, Glover, & Chittka,
483 2007), in bee-pollinated species with overlapping flowering periods, an association between
484 chromatic contrast and reward could be a way to promote flower constancy and to prevent
485 heterospecific pollen deposition. Optimal nectar concentration depends on feeding
486 mechanism and is approximately 35% for flowers pollinated by bees (Kim, Gilet, & Bush,
487 2011). Linking chromatic contrast to nectar concentration, bees are thought to make correct
488 decisions when visiting flowers in order to maximize energy intake rates. However, the
489 compound eyes of bees possess a low resolution for small flowers and consequently, bees
490 only appear to perceive the chromatic contrast of individual flowers when they are very close
491 to them (Hempel de Ibarra et al., 2015). Given that many flowers in our community are small
492 (mean size 18mm), the association between chromatic contrast and nectar concentration is
493 likely to be particularly important at close viewing distances. Unfortunately, no pollen
494 quality parameter was studied in our research, but since the nutritional value of pollen has
495 been reported to be selected by pollinators (Ruedenauer et al., 2019), pollen nutritional
496 quality might also be signalled by any floral colour parameter.

497 To our knowledge, the relationship between nectar offer and colour as perceived by bees has
498 been explored only in five communities. In three of these (including the present one), some
499 degree of association was found between both parameters (Giurfa, Núñez, Chittka, &
500 Menzel, 1995; Kantsa et al., 2017), whereas no relationship was detected in the other two

501 (Shrestha et al., 2020). We do not know any other study, aside from the present one, which
502 explores this kind of relationships for pollen offer at community level. Due to the fact that
503 few studies address these relationships and because of the existence of certain methodical
504 differences among them, it is difficult to establish the factors driving inter-community
505 differences, but those relationship would appear to be community specific.

506

507 4.4. Shape is negligible with regard to explaining rewards

508 Lastly, flower shape, another important visual signal in pollinator attraction (Gómez,
509 Perfectti, & Camacho, 2006; Gong & Huang, 2009; Møller & Eriksson, 1995; Møller &
510 Sorci, 1998), exhibited no significant association with any rewards in our community when
511 the regression was controlled by phylogeny. In contrast, corolla shape has been found to
512 constitute an honest signal to pollinators in some species at intraspecific level (Gómez &
513 Perfectti, 2010). In our community, we sampled a large amount of both radial and bilateral
514 species from different families, finding that sample size is probably not the cause of this lack
515 of association. The evolution of bilateral flowers is considered to be a key angiosperm
516 innovation, because they restrict the direction of approach and movement of pollinators on
517 flowers, thus increasing accurate pollen placement on stigmas (Neal, Dafni, & Giurfa, 1998;
518 Sargent, 2004). In contrast, radial flowers do not restrict access to rewards and usually
519 receive visits by many insect orders, some of these inefficient pollinators which act as nectar
520 or pollen thieves (Faegri & van der Pijl, 1979; Neal et al., 1998). This has given rise to the
521 theory that bilateral flowers invest less in producing pollen, which is a very expensive reward
522 (Hargreaves, Harder, & Johnson, 2009; Nicholls & Hempel de Ibarra, 2017), and that they
523 provide more abundant nectar, which is cheaper to produce in terms of energy (Heil, 2011;
524 Simpson & Neff, 1983). However, in the Mediterranean Basin, nectar is also expensive to
525 produce due to water limitations (Petanidou & Smets, 1995), and this could limit nectar

526 production.

527

528 Concluding remarks

529 In conclusion, in the community studied naïve bees might visit flowers driven by their innate
530 preferences for colour (Raine & Chittka, 2007), but following a learning process, it is
531 expected that their foraging decisions come to depend on floral signals that are honestly
532 associated with rewards, hence increasing constancy on highly rewarding flowers. Our study
533 clearly shows that, at plant community level, flower size honestly signals the quantity of
534 rewards and likely represents the most important cue for bees at greater distances. In contrast,
535 flower colour indicates a nectar quality parameter, i.e. nectar concentration. At shorter
536 distances, bees might be employing chromatic contrast to predict nectar concentration.

537 The relationship between visual signals and rewards may indicate an evolutionary history of
538 floral adaptation to the most effective pollinators in the Mediterranean Basin. This could be
539 applied to chromatic contrast, a parameter perceived specifically by bees. However, the
540 relationship between flower size and reward could be a simple consequence of either a higher
541 resource allocation in the larger flowers (Cohen & Shmida, 1993) or a variation in the mating
542 system, as predominantly selfing species frequently possess small flowers and produce little
543 pollen or nectar (Sicard & Lenhard, 2011). If the mechanical adjustment between flower and
544 visitor relative sizes implies that larger flowers are more successful when visited by larger
545 visitors, then the relationship between flower size and reward might be adaptive (Cohen &
546 Shmida, 1993; Herrera, 1985). Some studies have suggested that big bees, which have a
547 higher energy expenditure than small ones (Heinrich & Raven, 1972), prefer large flowers,
548 which provide greater rewards (Heinrich & Raven, 1972; Herrera, 1985). Indeed, at the
549 species level, however, some studies show that larger flowers are more successfully
550 pollinated by larger visitors due to a matching between bees and flowers (Galen & Newport,

551 1987; Stout, 2000); there is a need to demonstrate this relationship at community level.
552 Whatever may be the case, if the existence of honest associations in the community studied
553 implies an increase in floral constancy by bees, then a lower heterospecific pollen deposition
554 and higher fitness levels can be expected in bigger flowers and in flowers presenting a higher
555 chromatic contrast. However, there is a need to investigate the influence of these associations
556 in maintaining floral constancy and plant fitness at community level. Lastly, our study has
557 only focused upon visual signals, but olfactory signals can also play an important role in
558 plant-pollinator interactions. The integration of flower colour and scent as perceived by bees
559 found in another Mediterranean community (Kantsa et al., 2017), and the association
560 between visual signals and rewards found in the present study, highlight the existence of the
561 floral integration that can be perceived and learnt by bees, and this integration can therefore
562 be subjected to selection.
563

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988

989 SUPPORTING INFORMATION

990 TABLE S1. Multivariate phylogenetic model without considering *Cistus ladanifer*.

991 TABLE S2. Non-significant phylogenetic regressions.

992 TABLE S3. Multivariate phylogenetic model including floral display.

993 FIGURE S1. Phylogram of plants in the study community.

994 FIGURE S2. Phylogenetic construction of other floral traits.

995

996

997 CAPTIONS OF FIGURES

998 FIGURE 1. a) Colour loci of flowers plotted in the bee visual space and photographs of
999 some of the studied species. b) Reflectance spectra of all the species studied in the
1000 Mediterranean community. The colour of each spectral line reflects human colour
1001 vision of the flowers.

1002 FIGURE 2. Phylogenetic construction of some floral traits of the studied species of the
1003 community (see Fig. S2 for other floral traits).

1004 FIGURE 3. Significant phylogenetic generalized least squares regressions among floral traits
1005 of the studied community.

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1010 TABLE 1. Variability of floral traits in species pollinated by bees in a Mediterranean

1011 community. CV: coefficient of variation expressed as per-unit.

1012

Floral Traits	Mean \pm s.e.	Min - Max	CV
Flower size (mm)	18.26 \pm 1.4	1.5 - 95	0.73
Floral display	1043 \pm 371	1 - 12065	2.3
Brightness contrast	0.500 \pm 0.026	0.003 - 1.1159	1.4
Spectral purity	1.708 \pm 0.05	0.601 - 4.709	0.314
Green contrast	0.190 \pm 0.01	0.002 - 0.35	0.517
Reflectance amplitude	0.272 \pm 0.01	0.04 - 0.62	0.413
Chromatic contrast	0.228 \pm 0.01	0.07 - 0.5	0.402
Sugar concentration ($^{\circ}$ Brix)	28.98 \pm 3.6	10.6 - 100	0.84
Sugar mass per flower and day (μ g)	262.84 \pm 56.7	0 - 3008	2.0
Number of pollen grains per flower	102715 \pm 22935	119 - 1330295	1.95
Pollen volume per flower (mm^3)	1.28 \pm 0.42	0.002 - 30	2.94

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1018 TABLE 2. Phylogenetic signal for floral visual traits and rewards of 98 entomophilous

1019 species in a Mediterranean community.

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Floral traits	λ	$p_{\lambda=0}$	$p_{\lambda=1}$	95%CI
Continuous variables				
Floral display	0.362	0.2287	1	0.000 - 1
Flower size	0.230	0.0046	<0.0001	0.049 - 0.484
Chromatic contrast	0.322	0.0164	<0.0001	0.044 - 0.612
Green contrast	0.067	0.7817	<0.0001	0.000 - 0.577
Spectral purity	0.090	0.2069	<0.0001	0.000 - 0.323
Brightness contrast	0.434	0.0440	<0.0001	0.006 - 0.753
Reflectance amplitude	0.702	<0.0001	<0.0001	0.389 - 0.875
Sugar concentration	0.878	<0.0001	<0.0001	0.739 - 0.949
Sugar mass	0.009	0.91213	<0.0001	0.000 - 0.277
Pollen grain number	0.726	0.0014	<0.0001	0.400 - 0.870
Pollen volume	0.107	0.1005	<0.0001	0.000 - 0.301
Categorical variables				
Nectar presence	0.922			
Symmetry	1.000			
Bee colour	0.625			

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1023 TABLE 3. Significant phylogenetic generalized least squares regressions among floral traits
 1024 of 98 bee-pollinated species in a Mediterranean community.

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Dependent variable	Independent variable	F-statistic	DF	p-value	Adjusted R-squared	lambda
Sugar mass	Pollen number	5.448	1,69	0.022	0.0597	0.000
Sugar mass	Pollen volume	6.798	1,71	0.011	0.07453	0.000
Floral display	Brightness contrast	7.534	1,40	0.009	0.1375	0.000
Symmetry	Brightness contrast	9.576	1,96	0.002	0.080	0.000
Floral display	Bee colour	3.559	5,36	0.010	0.2387	0.000
Symmetry	Spectral purity	8.777	1,96	0.003	0.074	0.000
Flower size	Green contrast	4.093	1,93	0.045	0.03193	0.197

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1034 TABLE 4. Multivariate phylogenetic generalized least squares model between floral traits
 1035 and rewards of 98 species pollinated by bees in a Mediterranean community.

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 1037 **Sugar mass:** Adjusted $r^2 = 0.2004$, $F_{4,85} = 5.326$, $P = 0.0007$

Trait	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-25.7365	238.1267	-0.1081	0.9142
Flower size	18.4661	4.0693	4.5379	1.854e-05 ***
Green contrast	-43.2572	628.1678	-0.0689	0.9453
Brightness contrast	-56.2499	269.3752	-0.2088	0.8351
Chromatic contrast	-441.9439	692.9066	-0.6378	0.5253

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 1039 **Sugar concentration:** Adjusted $r^2 = 0.2351$, $F_{4,40} = 3.073$, $P = 0.026$

Trait	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.885998	10.511439	0.4648	0.644576
Flower size	-0.105261	0.082593	-1.2745	0.209858
Green contrast	11.308046	13.723844	0.8240	0.414842
Brightness contrast	12.151439	8.692147	1.3980	0.169824
Chromatic contrast	67.951162	24.311873	2.7950	0.007933 **

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 1041 **Pollen grains/flower:** Adjusted $r^2 = 0.4159$, $F_{4,69} = 12.26$, $P = 1.35e-07$

Trait	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	26172.49	103701.31	0.2524	0.8015
Flower size	6604.67	980.29	6.7375	3.965e-09 ***
Green contrast	50826.09	163847.54	0.3102	0.7573
Brightness contrast	-65169.37	77663.35	-0.8391	0.4043
Chromatic contrast	76443.62	198560.01	0.3850	0.7014

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 1043 **Pollen volume:** Adjusted $r^2 = 0.6833$, $F_{4,70} = 37.76$, $P = < 2.2e-16$

Trait	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.854093	1.128503	-1.6430	0.1049
Flower size	0.228981	0.019152	11.9557	<2e-16 ***
Green contrast	-2.570704	3.149196	-0.8163	0.4171
Brightness contrast	-1.526828	1.365145	-1.1184	0.2672
Chromatic contrast	0.982505	3.272178	0.3003	0.7649

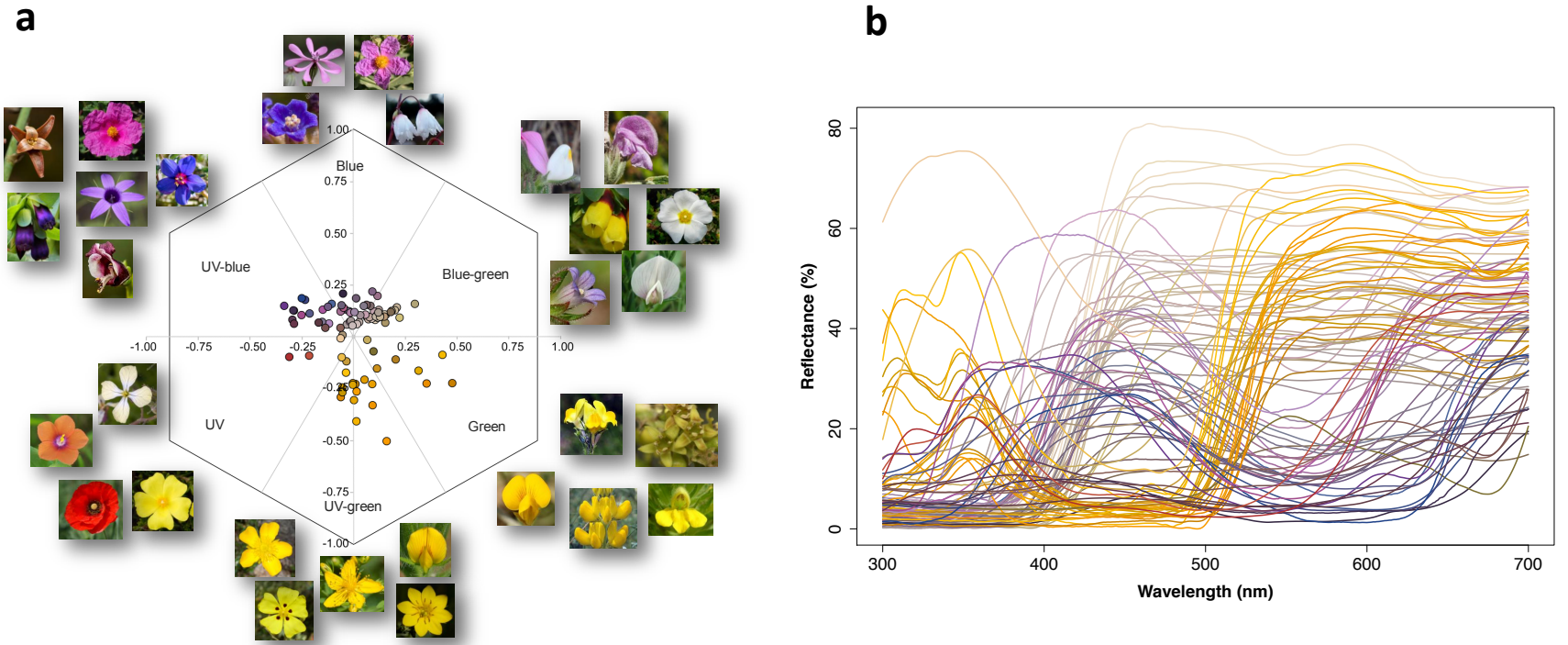
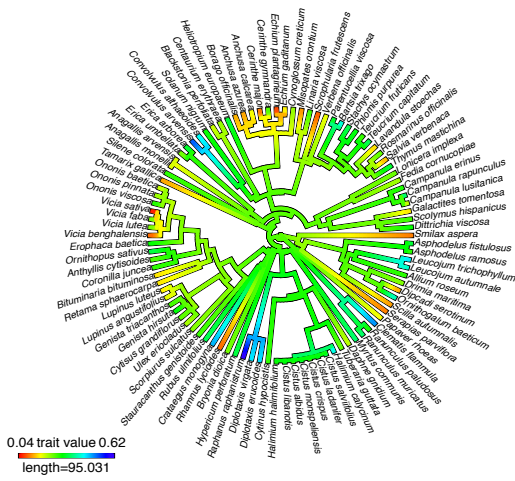


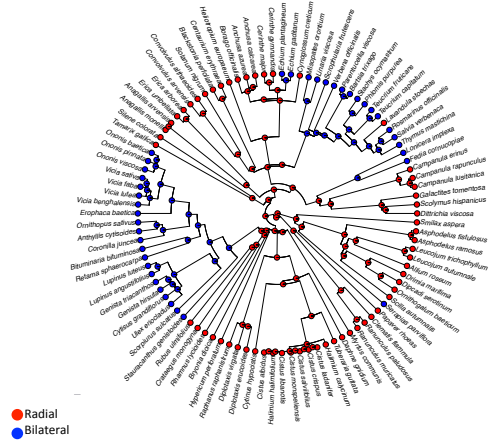
Figure 1

Figure 2

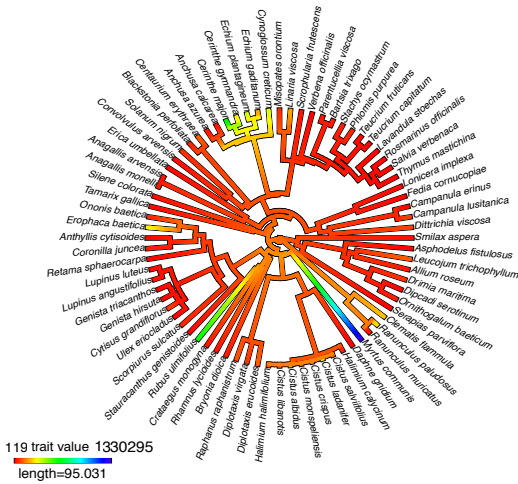
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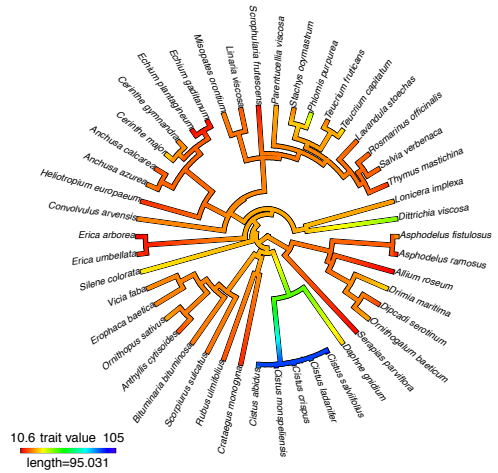
Symmetry



Pollen grain number



Sugar concentration



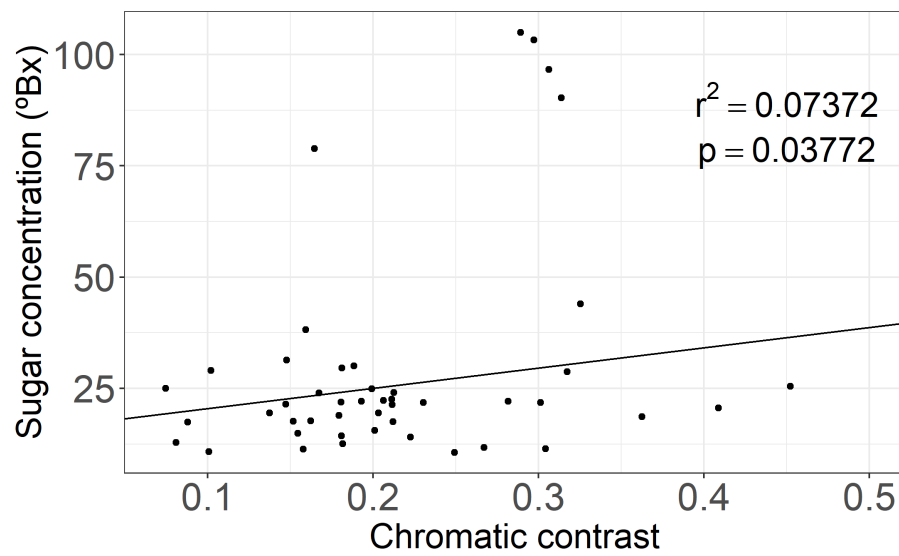
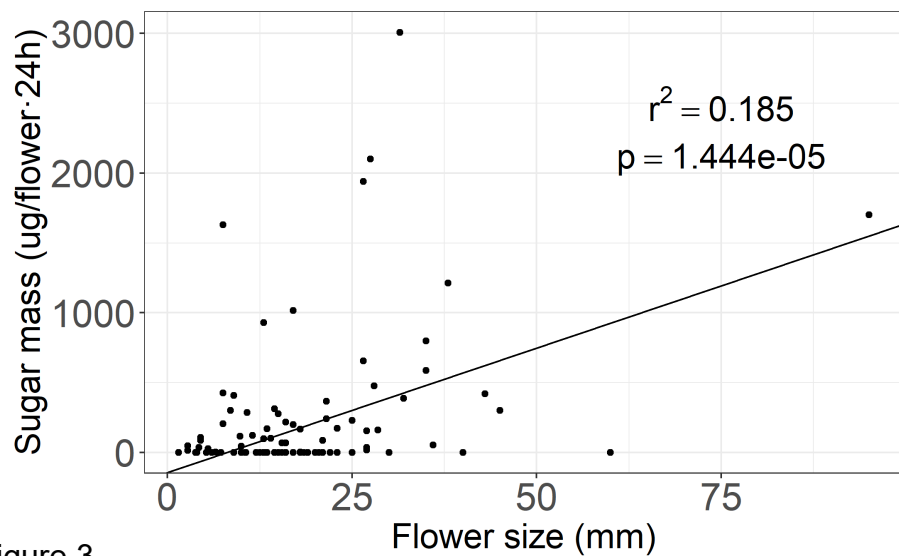
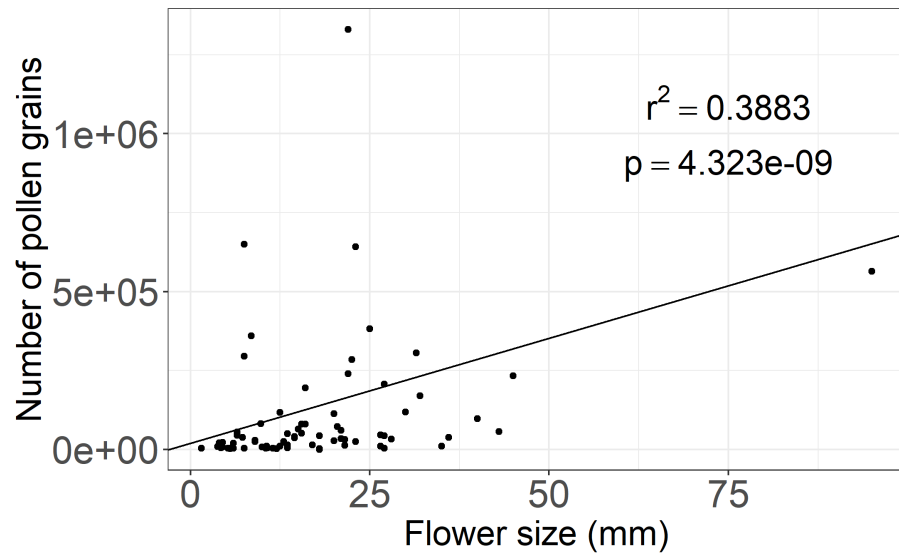
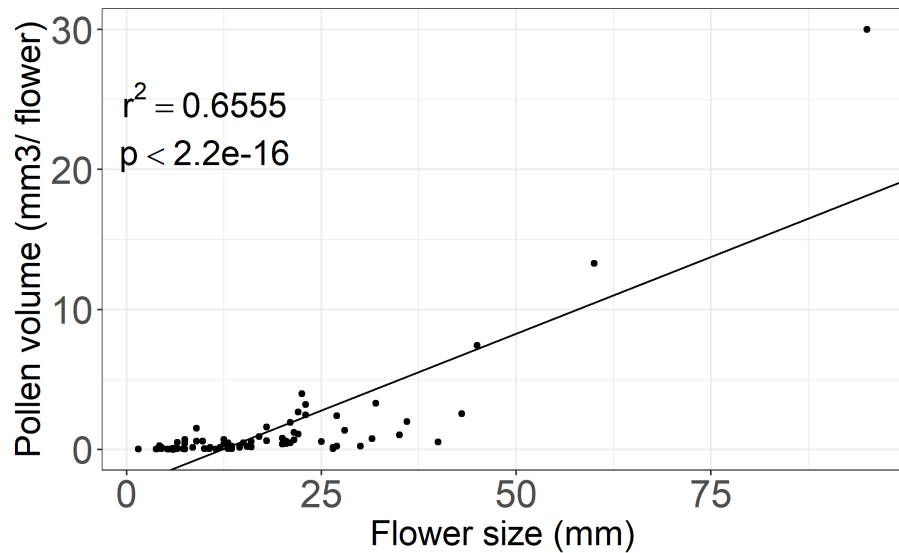


Figure 3