

Size Matters: Understanding the Conflict Faced by Large Flowers in Mediterranean Environments

Alberto L. Teixido^{1,4} · Miguel Barrio^{2,2} ·
Fernando Valladares³

¹ Departamento de Botânica, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, E-486, 30161-970 Belo Horizonte, Minas Gerais, Brazil

² Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, E-28049 Madrid, Spain

³ Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, MNCN-CSIC, Serrano 115 dpdo, E-28006 Madrid, Spain

⁴ Author for Correspondence; e-mail: alberto.lopez.teixido@gmail.com

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Abstract Flower size is a key trait in the reproductive ecology of animal-pollinated plants. However, pollinator-mediated selection does not always modulate this trait and environmental conditions and/or antagonist interactions may favor smaller flowers. We evaluate the occurrence of a large-flowered family in a hot and dry Mediterranean environment, mediated by a cost-benefit balance and a male–female conflict. Large flowers have sizeable benefits in terms of pollination and reproductive success and pollinators mediate selection through male function, but female fitness is context-dependent. High floral production and maintenance costs and florivore incidence in large flowers limit female function, which counteracts pollinator-mediated selection. Large flowers are highly costly in the Mediterranean and flower size is mediated by a sexual conflict between the benefits of male function and the costs of the female one. However, a short floral longevity, occasional pollen limitation and selection through maleness keep the existence of large flowers in these environments.

Keywords Cistaceae · Floral costs · Flower size · Pollinators · Male fitness · Female fitness

Introduction

Animal-pollinated plants include a large diversity of flowers, varying in color spectrum, shape and design, scent, longevity, size and display. Historically, numerous botanists and evolutionary biologists have greatly been interested in the study of the processes driving such a diversification (Sprengel, 1793; Darwin, 1862, 1877; Stebbins, 1950, 1970). As a general rule, scientific of both disciplines agree on conferring to pollinators a key role in the evolution of floral variability occurring in natural populations. This assumption is supported by the fact that zoophilous plants rely on pollinators for reproduction and flowers are the structures designed to this purpose. Flowers play an essential role in attracting pollinators, thus providing them energetic and nutritive rewards, whereas pollinators transfer pollen among plants within populations.

Overall, the taxonomic diversity of pollinators (birds, insects, mammals and reptiles), which includes a large morphological, functional and behavioral diversity, is matched to diversity of floral variation (Fenster et al., 2004; Aigner, 2005; Smith et al., 2008; Rosas-Guerrero et al., 2014; Gómez et al., 2015). Therefore, pollinators may potentially exert selection on floral traits in plant natural populations.

Flower size is a key trait in the reproductive ecology of animal-pollinated plants. This character is closely linked to pollinator attraction, as larger flowers are more easily detected (Bell, 1985; Ohashi & Yahara, 2001; Lázaro et al., 2013) and contain a greater amount of rewards, such as pollen and nectar (Cruden & Lyon, 1985; Herrera, 1992; Jones, 2001; Willmer, 2011). Flower size has consequently been related to increases in diversity (Andersson, 1988; Aigner, 2005; Cuautle & Thompson, 2010), frequency (Young & Stanton, 1990; Medel et al., 2007), number (Bell, 1985; Johnson et al., 1995; Liao et al., 2009), duration (Conner & Rush, 1996; Thompson, 2001; Nattero et al., 2011) and preference of floral visitors (Young & Stanton, 1990; Brody & Mitchell, 1997). Therefore, flower size greatly favors pollen transfer, thus increasing both male and female fitness (Bell, 1985; Conner & Rush, 1996; Aigner, 2005; Nattero et al., 2011; Barrio & Teixido, 2015). Consequently, many works have documented pollinator-mediated phenotypic selection towards larger flowers (e.g. Stanton et al., 1986; Galen, 1989, 1996; Totland, 2001; Maad & Alexandersson, 2004; Hodgins & Barrett, 2008; Sahli & Conner, 2011; Brothers & Atwell, 2014). Ultimately, processes of diversification in flower size should be followed by among-individual genetic variation so that evolution may occur. Indeed, natural plant populations show a high variability in flower size with a significant inheritability (Andersson & Widén, 1993; Galen, 1996; Ashman & Majestic, 2006). If pollinators exert selective pressures against small flowers and flower size is inherited, then flowers should show little variation in this trait (see Ushimaru et al., 2006). However, smaller flowers and flower size variation still remain within populations.

There are several possible explanations for the prevalence of smaller flowers and apparent variation in flower size. Overall, biotic factors other than pollinators (i.e. floral antagonists) together with abiotic factors such as resource availability and climate can potentially exert selective pressures on flower size and favor smaller flowers (Galen, 1999; Caruso et al., 2005; Strauss & Whittall, 2006; Campbell & Powers, 2015). The occurrence and strength of these factors as selective agents of flower size are mostly context-dependent in relation to environmental conditions and gender (i.e. pollen and/or resource limitation and their differential effects on male and female function; Ashman & Morgan, 2004). Theory predicts that smaller flowers will be potentially advantageous under benign pollination conditions, which reduce pollen limitation, and in hot and dry environments with low resource availability, especially in terms of water (Galen, 1999, 2005). Otherwise, larger flowers may be generally favored by increasing male fitness by means of higher pollen dispersal rates (Bell, 1985; Arista & Ortiz, 2007; Barrio & Teixido, 2015).

In this review, we aim to improve our understanding of possible causes that explain the subsistence of large flowers under hot and dry conditions. Full knowledge about the biotic and abiotic processes acting on the patterns of variation of flower size is essential to understand how plants achieve reproduction in these environments and, consequently, it is of extensive ecological and evolutionary importance. We begin our consideration with a brief introduction to the theoretical frameworks proposed to explain the

causes and consequences of the variation in flower size and the expected predictions in hot and dry ecosystems. Second, we show a potential conflict between large flowers and hot and dry conditions by using rockroses (Cistaceae) as a model system, a large-flowered family inhabiting a Mediterranean environment. Finally, we provide data of the extent and variation of the balance between costs and benefits in this study system as well as its consequences about reproductive success to, subsequently, discuss the ecological and evolutionary implications for flower size.

Theoretical Background

Why Does Flower Size Vary?

In a seminal paper, Galen (1999) explained in detail that a unilateral point of view of pollinator-mediated flower size evolution is probably oversimplistic. Selection on flower size is rather a pluralistic process in which not only pollinators are involved, but also some plant enemies (e.g. herbivores, parasites, predators) together with another alternative aspects of plant abiotic environment. In this regard, Galen (1999) proposed both the “resource-cost” and the “enemy-escape” hypotheses to explain the variation of this trait and improve in the understanding about why less-attractive flowers may be evolutionarily favored, thus balancing their low attraction to pollinators by means of a reduction in resource allocation as well as a greater protection from flower enemies. Therefore, an important facet in the maintenance of flower size variation is that those benefits acquired by pollinator attraction and subsequent pollen transfer may be counteracted by an increase in costs of such an attraction.

Flowers require a sizeable amount of resources directly assigned for their production and maintenance (i.e., direct costs; see Chapin, 1989; Ashman & Schoen, 1997; Teixido & Valladares, 2014a). Carbon, water and other nutrients are necessary to increase the pollinator attraction and reward as well as to maintain flowers physiologically active while remaining open, with showy petals, pigments, aromatic compounds and nectar (Cruden & Lyon, 1985; Pyke, 1991; Galen et al., 1993, 1999; De la Barrera & Nobel, 2004a; Witt et al., 2013). Accordingly, larger flowers require greater allocation of biomass and water for their construction (Ågren, 1988; Galen, 1999; Méndez & Traveset, 2003; Herrera, 2009; Halpern et al., 2010; Teixido & Valladares, 2013) as well as higher maintenance costs due to the high respiration and transpiration rates (Vemmos & Goldwin, 1994; Galen et al., 1999; Lambrecht & Dawson, 2007; Teixido & Valladares, 2014a).

A fundamental tenet in the resource economy of plants is that costs derived of the direct allocation of resources are translated into indirect costs (Gulmon & Mooney, 1986; see also Chapin, 1989), that is, in negative effects on other functions, such as the reproductive output. Andersson (1999, 2000, 2001, 2005) quantified indirect costs of floral attractiveness in diverse species. Overall, under controlled conditions of pollination, he found an increase in fruit and seed production in experimentally perianth-removed flowers in relation to unmanipulated control flowers. However, indirect costs of flower size were not taken into account, despite the evidence in this regard would provide a strong support to the prediction of Galen’s hypotheses (1999) based on resource allocation to flowers.

Larger-flowered plants have also to deal with additional costs imposed by antagonist animals, such as herbivores, parasites, seed predators and nectar robbers and thieves that obtain food and rewards from their floral visits without offering benefits to pollination (Shykoff et al., 1996; Krupnick et al., 1999; Irwin et al., 2001; Strauss & Whittall, 2006; Ruane et al., 2014). For example, floral herbivores (i.e., florivores) cause damage to open flowers and their structures (McCall & Irwin, 2006). Florivory incidence increases as traits of pollinator attractiveness do, thus increasing with flower size (Galen, 1999; Mosleh Arany et al., 2009; Oguro & Sakai, 2015). The resulting consume and degradation of flowers may reduce the reproductive success of the plant by (1) reducing the number of available flowers and/or permanence of smaller ones, (2) altering the attraction properties to pollinators or (3) directly consuming viable gametes (Schemske & Horvitz, 1988; Krupnick et al., 1999; McCall & Irwin, 2006; Cardel & Koptur, 2010; Althoff et al., 2013). From an evolutionary perspective, florivores may consequently exert negative selective pressures on flower size, making smaller flowers potentially advantageous against these floral enemies (Galen, 1999; Irwin et al., 2001; Irwin, 2006; Althoff et al., 2013).

What Does Theory Predict for Hot and Dry Environments?

Under hot and dry stressful conditions, animal-pollinated plants have to deal with two essential problems: first, water shortage may limit showiness of flowers and therefore pollinator attractiveness; second, high temperatures may induce higher floral physiological maintenance costs. Indeed, production and maintenance of corollas as showy structures to pollinators are particularly costly in terms of water (Galen et al., 1999; Lambrecht, 2013; Teixido & Valladares, 2014a). Many workers have provided experimental evidence for plants producing smaller flowers under drought conditions in a diverse range of species (Carroll et al., 2001; Elle & Hare, 2002; Caruso et al., 2005; Caruso, 2006; Halpern et al., 2010). Although those studies were not particularly focused on plants inhabiting hot and dry ecosystems and drought stress was artificially induced under controlled environmental conditions, results still show that xeric conditions may constrain selection for larger flowers by means a reduced soil water availability.

Additionally, flowers occurring in hot and dry environments may involve increased carbon costs and excessive evaporative demand. Galen and colleagues (Galen et al., 1999; Galen, 2000) reported that leaf photosynthetic rate at the time of flowering significantly declined with increasing corolla size in *Polemonium viscosum* under dry conditions, related to higher water use. Therefore, water demand by large corollas may influence leaf stomata closure, also constraining carbon gain (see also Lambrecht & Dawson, 2007). Likewise, floral overheating in hot climates can be damaging so transpirational cooling becomes crucial to minimize it (Patiño & Grace, 2002; Galen, 2005). However, water shortage in dry environments can lead to an inefficient thermoregulation. Heat and drought, acting together, can disrupt the normal performance of flowers, affecting both fruit and seed production (Konsens et al., 1991; Galen, 2000; Erickson & Markhart, 2002; Lambers et al., 2008; Fang et al., 2010).

Following these assumptions, minimizing floral water loss by reducing corolla size should be potentially advantageous for plants living in these environments (Galen, 2000, 2005; Elle & Hare, 2002; Herrera, 2005). In fact, here we exemplified this pattern

by surveying different plant communities occurring across a temperature and precipitation gradient in a Mediterranean ecosystem (Fig. 1). Species of communities inhabiting hotter and drier habitats significantly display smaller flowers than those ones flowering under wetter conditions (Fig. 1a). This pattern is interestingly taxonomic scale-independent as shows consistent repeatability both at family- and species-level, at least in Cistaceae, the family used as study system in this review (Fig. 1b, c). Hence, small flowers are not uncommon in hot and dry environments and seem to be the adaptative feature under these conditions.

However, some large-flowered plants do occur in hot and dry ecosystems. As a general rule, these species show adaptations to prevent overheating and excessive water loss. For example, nocturnal flowering and pollination are features of several caperbushes (*Capparis* sp.) of semi-arid areas (Rhizopoulou et al., 2006) and most large-flowered desert cacti (Valiente-Banuet et al., 1997; Fleming et al., 2001). Floral cooling mechanisms appeared to be critical for the reproductive success of large convulvaceous flowers in hot tropical environments (Patiño & Grace, 2002). Likewise, floral longevity is usually ephemeral according to fast fitness accrual rates occurring in large flowers under hot and dry conditions (Primack, 1985; Ashman & Schoen, 1994; Galen, 2005; Teixido & Valladares, 2015). Still, a few species display diurnal-pollination large flowers under hot and dry conditions. Therefore, these species represent a good model system to understand the selective pressures acting on flower size and why large flowers occur in these environments.

Study System: Large-Flowered Mediterranean Plants

Living and Flowering in a Hot and Dry Environment

High temperatures and water shortage over the summer generally characterize the climate in the Mediterranean region (Blondel & Aronson, 1999; Quézel & Médail, 2003; Thompson, 2005; see Fig. 2). Annual rainfall is concentrated into a small number of events along a short seasonal peak and soil moisture becomes decreasingly available during the drought period. As the progressive drought sets in, stomatal control is probably the most effective means of regulating water loss due to transpiration (Joffre et al., 1999). Stomatal closure may provide an effective control on water stress by allowing plants to increase water use efficiency during summer drought. Stomatal closure in response to water stress will also cause reduced gas exchange and thus reduce photosynthesis. However, reduction in transpiration may result in overheating, a problem that can be exacerbated by high solar irradiance and temperature. If excessive, such overheating can cause photo-inhibitory damage (Joffre et al., 1999). In addition to these constraints, Mediterranean plants have also to deal with a nutrient deficiency and a high incidence of herbivore insects (Thompson, 2005). Therefore, several conditions can thus simultaneously limit plant growth, survival and reproduction in these environments.

Under these circumstances, Mediterranean plants have developed an array of strategies to cope with such constraints. Specifically, phenologically and morphophysiological conservative resource use strategies and water use efficiency appear to be adaptative and to play a key role in these environments (Joffre et al., 1999; Valladares et al., 2000, 2008;

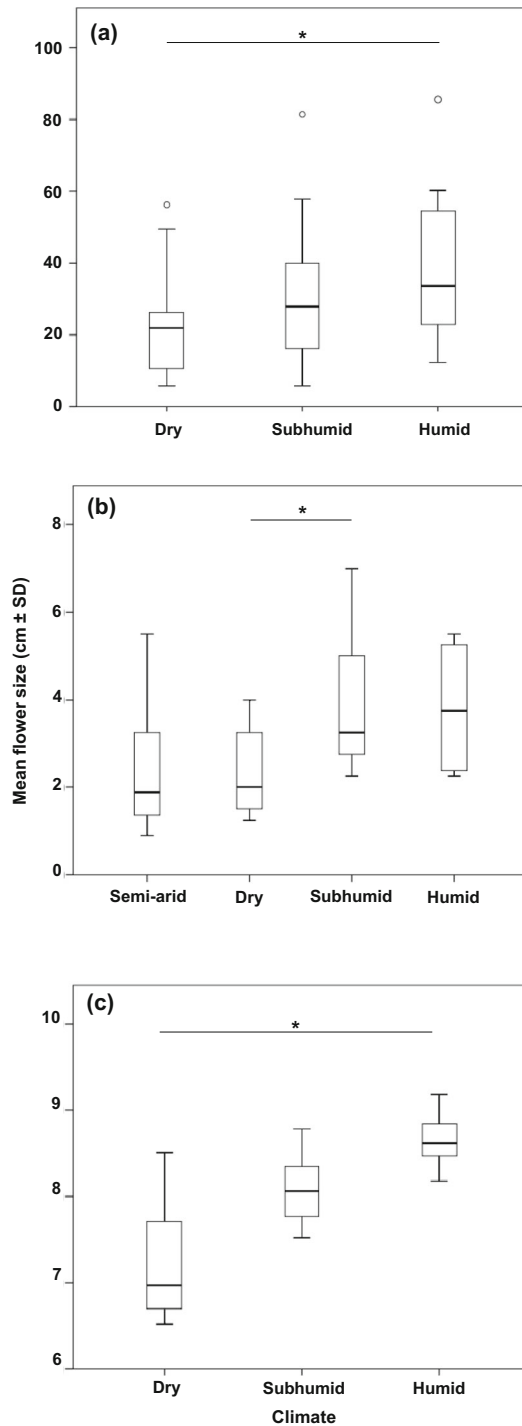


Fig. 1 Mean flower size in Mediterranean habitats differing in air humidity among (a) species communities (in this case, mean flower size is expressed in cm), (b) species of Cistaceae, and (c) populations of the largest-flowered species *Cistus ladanifer*. * $p < 0.05$

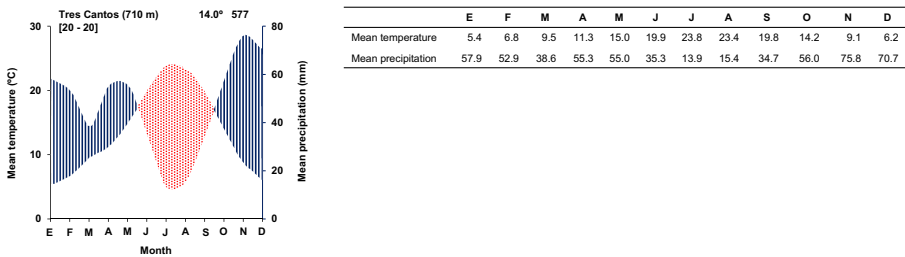


Fig. 2 Typical Mediterranean climatic diagram based on data recorded in Tres Cantos, Madrid, Spain, where several populations of *Cistaceae* were studied. $N = 40$ years (Ninyerola et al., 2005)

Larcher, 2000; Thompson, 2005; Zaragoza-Castells et al., 2008). Thus, tolerance and avoidance of drought stress are two non-independent characteristic features of Mediterranean vegetation. For example, sclerophyllous evergreen habit of trees and shrubs seems to be a well-fitted trait to Mediterranean stress conditions (Duhme & Hinckley, 1992; Valladares et al., 2004). The combination of morphological and physiological traits associated with sclerophylly may facilitate tolerance of negative turgor pressure under water stress as well as a higher degree of stomatal regulation (Duhme & Hinckley, 1992). The nutrient acquisition and allocation strategy of sclerophyllous species may also permit growth in a nutrient-poor soil and their chemical defence may assure long leaf lifetime. Additionally, one of the most characteristic features in the Mediterranean is the production of secondary volatile compounds, such as essential oils (Ross & Sombrero, 1991; Seufert et al., 1995). These chemical compounds may likewise mediate in defence against plant enemies and improve tolerance of water constraints and high solar radiation (Joffre et al., 1999; Thompson, 2005).

During the reproductive stage, plants may avoid and tolerate water stress by speeding up their development, shortening flowering duration (Larcher, 2000; Thompson, 2005; Aragón et al., 2008) and, occasionally, delaying the initiation of flowering until the rainy season to maximize water use efficiency (Blionis et al., 2001; Verdú et al., 2002). Many other species show an annual life history, avoiding the summer drought as dormant seeds and only germinating and flowering during the rainy season. Large and highly persistent seed banks in opposition to individual long life spans are not uncommon in the driest Mediterranean areas (Caballero et al., 2005; Aragón et al., 2009; Olano et al., 2012). Additionally, low investment in nectar reward is another common drought-avoiding feature in many Mediterranean plant species (Herrera, 1985; Petanidou et al., 2000; Potts et al., 2001). Likewise, insect diversity in the Mediterranean is high, so floral attractiveness has also to deal with greater plant-animal antagonist interactions. In several Mediterranean species, pre-dispersal flower, fruit and seed predators have been reported to have significant impact on fitness, and thus potentially constrain selection on flower size related to pollinators (Herrera, 2000, 2002; Gómez, 2003).

If conservative water use strategies are critical for the plants to flower in the Mediterranean region and this required process implies a sizeable water allocation in terms of floral production and maintenance under hot and dry conditions, water investment-based arguments to explain the potential advantages of smaller flowers in this ecosystem would be expected (Galen, 1999). Indeed, three studies in the Mediterranean ecosystem showed that flowers of *Narcissus triandrus* (Barrett et al.,

2004), *Rosmarinus officinalis* (Herrera, 2005) and *Cistus salvifolius* (Herrera, 2009) were smaller in hotter and drier populations. Our survey for this review goes further and shows that this pattern is not only apparent at specific-level, but also happens at both family- and community-level (Fig. 1). Therefore, variation in flower size follows an ecological gradient, increasing from warmer and drier to less stressful conditions. Likewise, antagonist-mediated selection has been reported to limit flower size in several Mediterranean species (Herrera, 1993, 2000, 2002; Gómez, 2003). From an evolutionary perspective, the presence of large and costly flowers contrasts with the expected mechanisms of “cost of resources” and “enemy-escape”, that would favour small flowers in these environments (Galen, 1999).

Cistaceae: a Large-Flowered Mediterranean Family

Cistaceae (so-called rockroses) is a family comprising eight genera (*Cistus*, *Crocanthemum*, *Fumana*, *Halimium*, *Helianthemum*, *Hudsonia*, *Lechea* and *Tuberaria*) and about 200 species of shrubs and herbs inhabiting temperate zones of Northern Hemisphere and South America (Arrington & Kubitzki, 2003). Its center of diversification is the Mediterranean region, especially in the Iberian Peninsula (up to 64 species), wherein occur widely distributed the five Mediterranean genera (i.e. *Cistus*, *Fumana*, *Halimium*, *Helianthemum* and *Tuberaria*; Muñoz-Garmendía & Navarro, 1993). The other three genera only appear in the American continent, from the middle east of the United States and southern Canada, to Central America, especially in Mexico, and temperate zones of South America (Arrington & Kubitzki, 2003). Around the Mediterranean region, species of this family usually occur in hot and open areas with rocky dry soils, calcareous or acidic, forming scrublands and herb understory of the sclerophyllous mixed formations dominated by *Pinus* and *Quercus* (Muñoz-Garmendía & Navarro, 1993; Arrington & Kubitzki, 2003).

Flowering occurs almost exclusively during the spring, at earliest in February, and can readily extend up to July (Muñoz-Garmendía & Navarro, 1993). There are some annual herbaceous species, but the vast majority are perennial and polycarpic shrubs. Flowers are hermaphrodites and typically chasmogamous, with five yellow, white or pink-purplish petals conforming a disc-shaped corolla. Anthesis occurs early in the morning and synchronously within populations (Herrera, 1992). Self-incompatibility is common across the family, but some herbs and smaller-flowered species can show self-pollination and cleistogamous flowers (Herrera, 1992; Talavera et al., 1993, 1997; Rodríguez-Perez, 2005; Aragón & Escudero, 2008; Guzmán et al., 2015).

Although flower size is somewhat variable, the perennial shrub genera *Cistus* and *Halimium* often show large flowers (Fig. 1c). Most interestingly, *Cistus ladanifer* is one of the largest-flowered species in the Mediterranean area, with diameters that can exceed 10 cm (Arrington & Kubitzki, 2003; Teixido et al., 2011). Stamens of these genera are usually numerous and their anthers contain large amounts of pollen grains, which is positively correlated with flower size (Bosch, 1992; Herrera, 1992; Arista & Ortiz, 2007). These species also contain high pollen-to-ovule ratios, consistent with outcrossing breeding systems (Bosch, 1992; Herrera, 1992). In fact, formal experimental studies have reported that these species are mostly self-incompatible and they depend on a vast spectrum of pollinators for reproduction (Brandt & Gottsberger, 1988; Bosch, 1992; Herrera, 1992; Talavera et al., 1993, 1997, 2001; Teixido &

Valladares, 2014b; Guzmán et al., 2015). Overall, these *Cistus* and *Halimium* large-flowered species constitute a model study system to exhaustively evaluate the selective pressures operating on flower size and the conflicts faced by large flowers in a hot and dry environment such as the Mediterranean ecosystem.

Here we provide observational and empirical data by reviewing those studies focused on large-flowered rockroses comprising surveys of pollinators, reproductive success, phenotypic selection, direct costs of floral production and maintenance in terms of carbon and water, indirect costs in terms of fruit and seed production, and florivory (Table 1). Overall, our review includes seven species of large-flowered Cistaceae showing among- and within-population variation in flower size and occurring across 18 different populations with contrasting climatic conditions. Additionally, we show unpublished data collected from our own research in the relation between resource allocation for floral production with flower size among 37 species of Cistaceae. We analyse the effect of such variations in flower size and environmental conditions on the benefit-cost balance of displaying large flowers and, consequently, its ecological and evolutionary consequences at three different levels. First, at interspecific level, i.e., among species with contrasting flower size. Second, at intraspecific level or among populations within of a particular species. Third, among individuals showing variation in flower size within populations.

Understanding the Matter: Ecology and Evolutionary Aspects

Balance Between Costs and Benefits

Pollinators and Reproductive Success. The interactions between large-flowered Cistaceae and pollinating agents show the generalist character of these species. Large and showy flowers are rewarded for the visit of a high number and diversity of pollinators, including ants, bees, bumblebees, beetles, flies and wasps of different size and behaviour (Bosch, 1992; Talavera et al., 1997, 2001; Teixido & Valladares, 2014b). Interestingly, the amount of pollinating visitors significantly increase with interspecific variation in flower size (Fig. 3). Bosch (1992) reported higher indexes of attractiveness in the largest-flowered species, *Cistus albidus*, among three coflowering *Cistus* with contrasting flower size. Based on Talavera et al.'s (2001) study with *Cistus libanotis* and data from our own research with *Cistus ladanifer* (Teixido & Valladares, 2014b; Barrio & Teixido, 2015), we calculated a mean attractiveness index for these species following the Bosch's (1992) methodology. A regression model for all the indexes of attractiveness on flower size for those five *Cistus* species reveals the significant benefits reached by larger-flowered species in terms of pollinator visit rates (Fig. 3). Specifically, a two-fold increase in flower size entails about an attractiveness index five-fold higher. Therefore, the largest-flowered species *C. ladanifer* shows a very beneficial attractiveness in relation to other smaller-flowered *Cistus* species.

Overall, a direct consequence of the numerous and diverse plant-pollinator interaction in *Cistus* is a double benefit in sexual terms, as these species are hermaphrodites. On the one hand, this favours a high set of fruit and seed production, which readily exceeds 80 % (Bosch, 1992; Talavera et al., 2001; Arista & Ortiz, 2007; Guzmán et al., 2011; Teixido & Valladares, 2014b). On the other hand, flowers have a great amount of

Table 1 Flower size, climatic data of the populations and type of study of every species used in this review. Each row corresponds with a different population, but for *Cistus ladanifer*, for which nine populations were used. In this case, populations with identical climatic data are the same, but they were studied in different years (2009, 2010 and 2011)

Species	Flower size	Type of study	Climate	References
<i>Cistus albidus</i>	4.9±0.3	Pollinators and RS (♀)	15 °C, 653 mm	Bosch, 1992
	5.3±0.5	Indirect costs	13 °C, 567 mm	Teixido & Valladares, 2013
	5.1±0.4	Maintenance costs	13 °C, 567 mm	Teixido & Valladares, 2014a
<i>Cistus ladanifer</i>	6.4±1.5	Pollinators and RS (♀)	16 °C, 563 mm	Talavera et al., 1993
	7.0±1.1	Florivory	14 °C, 520 mm	Teixido et al., 2011
	8.0±0.7	Florivory	12 °C, 771 mm	Teixido et al., 2011
	8.1±0.8	Florivory	11 °C, 820 mm	Teixido et al., 2011
	8.6±0.8	Florivory	9 °C, 865 mm	Teixido et al., 2011
	9.2±0.8	Indirect costs	13 °C, 567 mm	Teixido & Valladares, 2013
	9.2±0.7	Indirect costs	9 °C, 865 mm	Teixido & Valladares, 2013
	7.9±0.9	Maintenance costs	13 °C, 567 mm	Teixido & Valladares, 2014a
	9.3±0.9	Pollinators and selection (♀)	14 °C, 533 mm	Teixido & Valladares, 2014b
	9.1±0.8	Pollinators and selection (♀)	14 °C, 533 mm	Teixido & Valladares, 2014b
	8.6±1.1	Pollinators and selection (♀)	9 °C, 865 mm	Teixido & Valladares, 2014b
	8.8±0.7	Pollinators and selection (♀)	9 °C, 865 mm	Teixido & Valladares, 2014b
	8.1±0.9	Pollinators and selection (♂, ♀)	14 °C, 544 mm	Barrio & Teixido, 2015
	8.4±0.9	Pollinators and selection (♂, ♀)	11 °C, 899 mm	Barrio & Teixido, 2015
<i>Cistus libanotis</i>	Ca. 3 cm	Pollinators and RS (♀)	16 °C, 563 mm	Talavera et al., 2001
<i>Cistus laurifolius</i>	6.0±0.5	Indirect costs	9 °C, 867 mm	Teixido & Valladares, 2013
<i>Cistus monspeliensis</i>	2.2±0.1	Pollinators and RS (♀)	15 °C, 653 mm	Bosch, 1992
<i>Cistus salvifolius</i>	4.1±0.5	Pollinators and RS (♀)	15 °C, 653 mm	Bosch, 1992
	4.8±0.2	Selection (♂, ♀)	—	Arista & Ortiz, 2007
	4.7±0.1	Selection (♂, ♀)	—	Arista & Ortiz, 2007
	5.1±0.1	Selection (♂, ♀)	—	Arista & Ortiz, 2007
	—	Production costs	529 mm	Herrera, 2009
	—	Production costs	630 mm	Herrera, 2009
	—	Production costs	915 mm	Herrera, 2009
<i>Halimium atriplicifolium</i>	5.0±0.2	Indirect costs and selection (♀)	13 °C, 467 mm	Teixido, 2014

pollen grains and this noticeably facilitates their dispersal (Arista & Ortiz, 2007; Barrio & Teixido, 2015). In particular, this increased male and female reproductive output is sizeable in *C. ladanifer*, as flowers of this species produce a high pollen and ovule

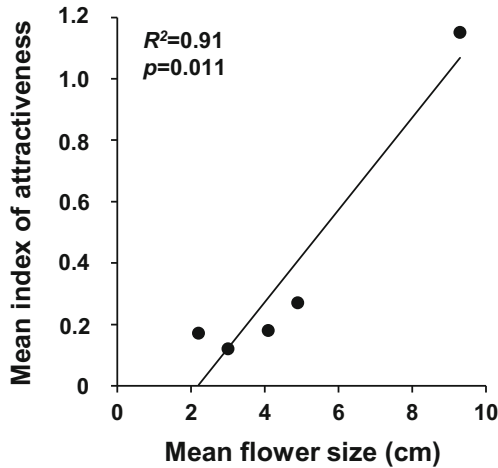


Fig. 3 Mean index of attractiveness for five *Cistus* species (*C. albidus*, *C. ladanifer*, *C. libanotis*, *C. monspeliensis* and *C. salvifolius*) with contrasting flower size. Indexes were calculated following Bosch (1992)

amount (Herrera, 1992; Talavera et al., 1993). This largely favours pollen dispersal and seed production, not only by increasing pollinator visit rates and diversity, but also by having more pollen and ovules available. Pollen production in this species can readily exceed 750,000 grains/flower whereas the number of ovules reaches up to 1500/flower (Talavera et al., 1993), which involves about a ten-fold increase in relation to other *Cistus* species (Herrera, 1992). Consequently, the values of male and female reproductive success in *C. ladanifer* are particularly high.

The abundance of pollinating insects visiting flowers and, subsequently, the high fruit and seed production, entails that there is an adequate pollen quantity deposited on stigmas. This is also noteworthy since may happen in only a few hours, as flowers generally last one day open (Teixido & Valladares, 2014c). In fact, when flower size was experimentally reduced in *C. salvifolius* and *C. ladanifer*, flowers still produce high percentages of fruits and seeds (Arista & Ortiz, 2007; Barrio & Teixido, 2015). Therefore, an additional advantage of flower size is that pollination visitation is promptly enough to fertilize all the ovules and thus easily reaching a high reproductive success.

However, pollen quantity limitation is not an uncommon pattern in large-flowered rockroses and here is where flower size variation within-populations becomes relevant. This variation plays a key role as larger-flowered individuals significantly increase pollinator visit rates (Teixido & Valladares, 2014b; Barrio & Teixido, 2015). In addition, flower size is positively related to ovule number (Herrera, 1992). Thus, smaller-flowered individuals not only have less available ovules, but also receive less pollen. Although pollinators are abundant and diverse, visitation decreases in relation to larger flowers and may not be sufficient to fertilize all the ovules. This involves that in pollen-limited populations pollinators may potentially exert selection towards larger flowers through female fitness (Arista & Ortiz, 2007; Teixido & Valladares, 2014b; see also Table 2). Therefore, fruit and seed production in larger-flowered individuals may be even more favoured by means a differential increase of offspring.

The positive relationship between flower size and pollinators also entails benefits to male function. Larger-flowered individuals have more anthers, disperse higher pollen amounts and could potentially sire a higher number of seeds. However, this hypothesis has not been accurately tested in our study system, mainly due to the complexity of measuring male function in natural populations. Molecular analysis with genetic markers, including DNA extraction and genotyping are needed to record direct estimates of male reproductive success (reviewed in Conner, 2006). Though indirect methods such as the amount of dispersed pollen do not necessarily imply paternity success, pollen dispersal is a representative component of male success and is a useful measure to disentangle the mechanisms, the strength and the direction of phenotypic selection through this sex (Snow & Lewis, 1993; Maad & Alexandersson, 2004; Kuriya et al., 2015). In this regard, formal studies with *C. salvifolius* (Arista & Ortiz, 2007) and *C. ladanifer* (Barrio & Teixido, 2015) have shown that pollinator-mediated selection towards larger flowers is frequent and intense through pollen dispersal (Table 2).

Table 2 Type of selection and standardized selection gradients for flower size in three large-flowered species of Cistaceae on male (dispersed pollen) and female fitness (fruit set, seed number and seedling mass) at each of the studied populations and years. Selection gradients with significant *P*-values are marked in bold. Linear (β') and quadratic (γ') coefficients \pm SE are shown for positive linear (positive β') and non-linear (stabilizing; negative γ') selection, respectively. Adapted, with permissions, from: ¹Teixido & Valladares, 2014b (© John Wiley and Sons); ²Barrio & Teixido, 2015 (© Springer); ³Arista & Ortiz, 2007 (© John Wiley and Sons); ⁴Teixido, 2014 (© Oxford University Press)

Species	Population	Year	Fitness measures			
			Male fitness		Female fitness	
			Dispersed pollen		Fruit set	Seed number
<i>Cistus ladanifer</i> ^{1,2}	Tres Cantos	2010	—	Stabilizing -0.12 \pm 0.06	Not significant	—
		2011	—	Stabilizing -0.09 \pm 0.04	Not significant	—
		2013	Positive 0.09 \pm 0.05	Not significant	Not significant	—
	Canencia	2010	—	Not significant	Positive 0.12 \pm 0.04	—
		2011	—	Not significant	Not significant	—
	El Escorial	2013	Positive 0.15 \pm 0.05	Not significant	Positive 0.12 \pm 0.04	—
<i>Cistus salvifolius</i> ³	El Membrillo	2004	Positive 0.20 \pm 0.03	Not significant	Positive 0.22 \pm 0.04	Not significant
	El Pozo	2004	Positive 0.17 \pm 0.03	Not significant	Not significant	Not significant
	Pasá La Zorra	2004	Positive 0.33 \pm 0.04	Not significant	Not significant	Not significant
<i>Halimium atriplicifolium</i> ⁴	Valdecorzas	2011	—	Stabilizing -0.13 \pm 0.05	Not significant	—

Direct Costs: Floral Production and Maintenance. However, the production of large and showy flowers requires a sizeable resource allocation and their maintenance a high energetic demand and water uptake to remain physiologically active. In Cistaceae, sexual structures (carpels and stamens) comprise important amounts of nitrogen and phosphorous, whereas perianth (calix and corolla) require a high investment in terms of carbon (dry mass) and water (fresh mass) (Herrera, 2009; Teixido & Valladares, 2013; Teixido, 2014). In our survey of 37 species of rockroses, we detected that floral resource allocation in terms of dry mass and nutrients exponentially increases with flower size (Fig. 4). This means that the investment in floral production follows an allometric pattern, i.e., larger flowers not only are more costly for being larger, but also allocate more resource by unit of area. Likewise, attractiveness to pollinators is correspondingly expensive, as corollas involve about one-third of floral dry mass with a high investment of carbon (Teixido & Valladares, 2013; Teixido, 2014) and about a half of allocation in terms of fresh mass (Herrera, 2009). Specifically, the largest-flowered species (*C. ladanifer*) requires up to a five-fold more resource allocation to petals than other large-flowered *Cistus* (Teixido & Valladares, 2013). Interestingly, investment to floral attractiveness may also show an intraspecific variation in relation to habitat type. Herrera (2009) found that upland populations of *C. salviifolius* displayed larger and heavier flowers with greater fresh mass allocation to corollas than lowland, drier populations. Therefore, water conservation-based local selective pressures may probably maintain considerable levels of intraspecific floral variation and reduce flower size in hotter and drier sites.

In terms of floral maintenance, water costs related to evapotranspiration are also high and allometrically increase in larger-flowered species, especially under hotter and drier conditions (Teixido & Valladares, 2014a). As shown in Fig. 5, mean floral transpiration rates in *C. ladanifer* are about six-fold higher than those of *C. albidus*, whereas difference in flower size between both species is about a two-fold magnitude. At intraspecific level, larger-flowered individuals of *C. ladanifer* significantly transpire

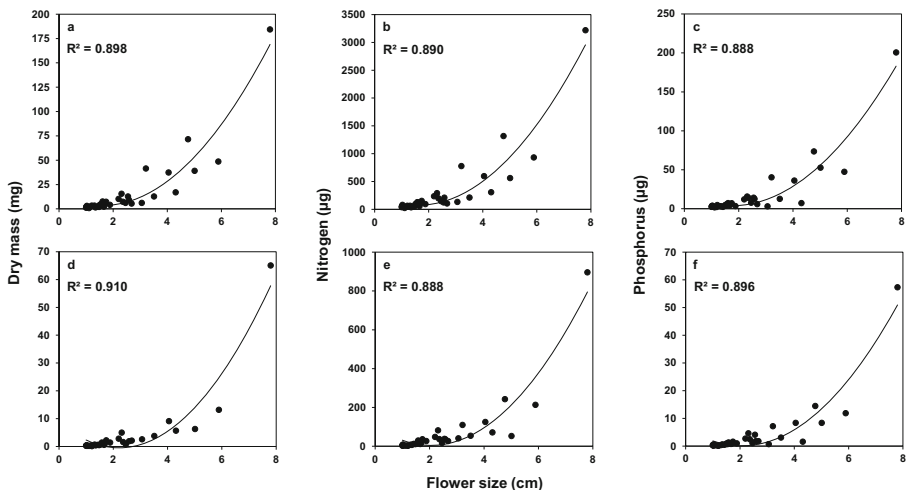


Fig. 4 Allometric relationships between resource allocation in terms of dry mass and nutrients (nitrogen and phosphorous) to floral structures (a, b and c) and corolla (d, e and f) with flower size across 37 species of Cistaceae with contrasting flower size. $p < 0.05$ in all cases

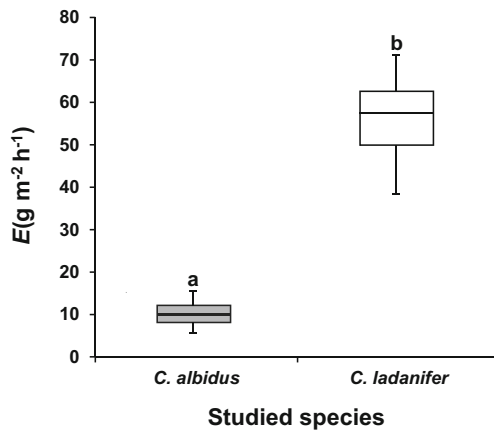


Fig. 5 Box plots of variation in transpiration rates of corollas in *C. albidus* and *C. ladanifer*. Different letters indicate significant differences ($p < 0.05$)

more and, additionally, tend to spend about four-fold more water in sunny days than during cloudy days (Teixido & Valladares, 2014a). In fact, corollas of *C. ladanifer* reach transpiration rates similar to those of large-flowered cacti inhabiting arid climates (Nobel & De la Barrera, 2000; De la Barrera & Nobel, 2004b). Only the transpiration of these corollas, without considering other floral structures, entails the use of two litres of water during the flowering period. On a similar organ surface area basis, corollas also require more than a half of leave water use, which is noticeable because corollas remain open and functional only about 6 h (Teixido & Valladares, 2015).

In addition to water costs, floral energetic demands require maintenance costs in terms of carbon. Net exchange rates in petals are negative, which indicates low or non-existent photosynthetic production in relation to carbon loss mediated by respiration (Teixido & Valladares, 2014a). Respiratory demands recorded in corollas of *C. ladanifer* ($-0.91 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) reach up to 64 % of leaf respiration rates ($-1.42 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) per unit of area and time and quadruple those of species inhabiting cold habitats (Galen et al., 1993; Teixido & Valladares, 2014a). Higher respiration rates are expected to happen in hotter environments because plant respiration increases as a function of temperature (Atkin & Tjoelker, 2003). Still, floral net carbon exchange rate in *C. ladanifer* suggests high respiratory demands in large-flowered Mediterranean species. Besides petal respiration, flower size may also involve additional costs, such as nectar production and calix, carpel and stamen respiration.

Indirect Costs: Negative Effects on Reproductive Output. Direct resource allocation to floral production and maintenance impose significant limits to female reproductive success. Therefore, there also are indirect costs in terms of fruit and seed production, as detected under controlled conditions of pollination and experimentally removing floral attractiveness structures (Andersson, 1999, 2000, 2001, 2005). In Cistaceae, indirect costs were noticeable as the relative gain of fruits in petal-removed flowers ranged 11–33 % and that of seeds 8–16 % in relation to control unmanipulated flowers (Fig. 6). This range of variation was significantly related to interspecific and intraspecific differences in flower size. Furthermore, the intensity of

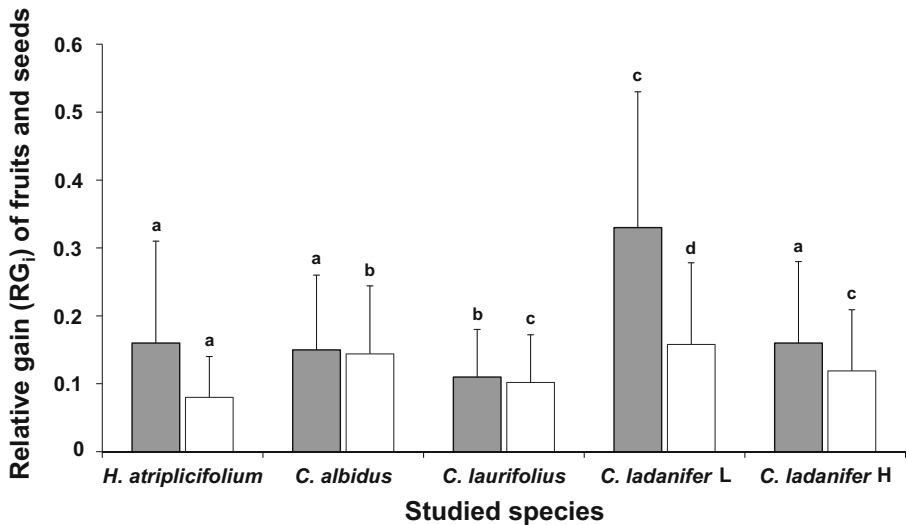


Fig. 6 Comparison of relative gain of fruits (grey bars) and seeds (white bars) for petal-removed and control flowers among different species of Cistaceae. Different letters between relative gain of fruits (grey bars) and between relative gain of seeds (white bars), respectively, indicate significant differences among species using an unequal HSD post hoc test ($p < 0.05$)

relative gain of fruits showed significant differences with local climatic conditions. For example, *C. ladanifer*, the largest-flowered species, had the highest rates of relative gain of fruits and seeds, and this gain showed a two-fold increase in terms of fruits in the driest population (Fig. 6). For the smaller-flowered species with less interspecific variation in flower size, those occurring in drier sites showed a significant increase of reproductive output between petal-removed and control flowers in relation to wetter sites, at least in terms of fruits (i.e. *C. albidus* and *H. atriplicifolium*; Fig. 6; see also Table 1 for mean specific flower size and local climatic conditions).

Indirect costs for fruit set also increased with flower size for all four studied species (Teixido & Valladares, 2013; Teixido, 2014). Most interestingly, the relationship between relative gain of fruits and flower size was also greater in the larger-flowered species in the sympatric coflowering pair *C. ladanifer*–*C. laurifolius* (Teixido & Valladares, 2013). Overall, these results suggest that the functional and physiological maintenance of corollas involves indirect costs in terms of fruit and seed production. This is especially relevant in larger-flowered species and/or under the driest and hottest, most stressful conditions. Therefore, petal-removed flowers may increase their reproductive output by saving water and other resources, such as carbon, to maintain petals physiologically active.

Ecological Costs in Terms of Florivory. Lastly, larger flowers entail additional costs to production and maintenance by increasing florivory incidence, which could involve more limitations to fruit and seed production. Besides, pollen consume and degradation of floral attractiveness derived from florivore damage may constrain male fitness. However, nothing is known about the effects of florivory on reproductive output or as selective mechanism on flower size in Cistaceae or any large-flowered Mediterranean species. To our best knowledge, Teixido et al. (2011) reported the only

study about florivore incidence in relation to flower size variation focused on the large-flowered *C. ladanifer*. Several ant species picking stamens and beetles consuming petals and pollen were the main florivores (Fig. 7) and the incidence of florivory was significantly and positively influenced by flower size in three populations, with florivory probabilities of approximately 18–35 % on largest flowers. Although the impact of this incidence on fitness was not studied, the negative effects of florivores on reproductive output and their selective pressures on flower size reported by several studies (Galen, 1999; Irwin et al., 2001; Irwin, 2006; Althoff et al., 2013; Ruane et al., 2014) lead to suppose that smaller flowers may be potentially advantageous against these enemies.

Ecological Context and the Evolutionary Battle of the Sexes

Overall, we have pointed out that flower size in our study system is adjusted to a cost-benefit balance, but this process is closely linked to sex. Sexual allocation theory suggests that selection on flower size should be stronger through male fitness whereas the female one is resource-limited (“male function” hypothesis, see Wade, 1979; Burd & Callahan, 2000; Jones, 2008). Although this general statement is controversial and seems to be more dependent on ecological context (see Ashman & Morgan, 2004 for details), this is the pattern commonly reported in Cistaceae (Arista & Ortiz, 2007; Barrio & Teixido, 2015). Indeed, despite a predominance of a directional and positive phenotypic selection towards larger flowers through pollen dispersal, the costs derived from Mediterranean stressful conditions wherein rockroses occur may reduce female reproductive success and, ultimately, impose constraints to flower attractiveness.

In Cistaceae, it is not uncommon the absence of phenotypic selection on flower size through female fitness components (Arista & Ortiz, 2007; Teixido, 2014; Teixido & Valladares, 2014b; Barrio & Teixido, 2015). Furthermore, resource limitation resulting from floral physiological maintenance and subsequent indirect costs in terms of fruit and seed production (i.e. female fitness) involve processes of stabilizing selection on flower size (Teixido, 2014; Table 2). This implies that must exist a combined action of pollen limitation with resource limitation and subsequent floral costs. In this regard, small increases in flower size within a given population would increase fruit and seed set by reducing pollen limitation until flower size becomes too large and, then, elevated floral costs counteract the benefits of high rates of pollen deposition, thus reducing fruit and seed production.

When both sexes have different optima for those traits related to reproductive success, there may be a sexual conflict giving rise to traits in equilibrium (Chapman, 2006). Therefore, pollinator attractiveness itself in natural populations of Cistaceae does not always involve selection towards larger flowers and evolution on this trait may be limited by opposite evolutionary pressures of both sexes that could lead to sexual selection conflicts on flower size. Specifically, these opposite selective pressures could be also acting on female fitness components, related to the strength of pollen and resource limitation and, ultimately, influenced by an ecological context. We detected that flower size showed temporal variation in two populations of *C. ladanifer* in response to phenotypic selection on fruit set or seed number in the year before,



Fig. 7 Some florivores such as (a) ant species picking stamens and (b) beetles eating petals cause damage to flowers of *C. ladanifer* by means of pollen consume and degradation of attractiveness, respectively

increasing flower size when there was positive directional selection and decreasing when was stabilizing (Teixido & Valladares, 2014b). Hence, total selection exerted on flower size in this large-flowered species may depend strongly on whether plants are more pollen or resource limited in their female reproduction, respectively. This pattern suggests the important role that female function, the more resource-limited gender, plays in the plasticity and temporal variation of flower size and in the potential of buffering costs and modulating this trait in Cistaceae.

Concluding Remarks

Understanding how large flowers occur in hot and dry environments such as the Mediterranean, an anomalous trait in this ecosystem, is of extensive ecological and evolutionary importance. Flowers are the most diverse structures produced by angiosperms and knowledge about plant-animal and plant-environment interactions are essential to explain their patterns of diversification and the mechanisms, limitations and processes carried out to achieve reproduction. Additionally, increases in temperature and decreases in precipitation induced by climate change in the Mediterranean could disrupt the plant-pollinator interactions and damage flowers, thus limiting their reproductive success and, consequently, imposing selective constraints to flower size. There are abundant evidence about the growth and survival limitations to which Mediterranean plants are subjected. However, little is known about flowering costs and the effects of flower size, an additional cost potentially awkward for plants inhabiting this ecosystem. Considering this knowledge gap, we addressed this question by reviewing the scarce experimental and observational data on this topic using a large-flowered family to reach a broader perception about the benefits, costs and functional limitations of large flowers in this stressful environment.

Here, we confirm that flower size is a relevant trait in animal-pollinated hermaphroditic plants as large flowers are exposed to strong selective pressures imposed by a cost-benefit balance and a sexual conflict in a stressful environment. Overall, high reproductive benefits achieved by large-flowered Cistaceae can be counteracted by the environmental stress inherent to the Mediterranean ecosystem, which limits the advantages of flower size (especially through the female fitness). Therefore, our review supports the idea that the relative strength and direction of selection on flower size is not only pollinator-dependent. However, pollinator-mediated selection for increasing flower size through both components of fitness is feasible, keeping large flowers in this system. Specifically, we have identified several conclusive assumptions as well as several open questions that deserves future research:

- (1) Large flowers obtain benefits in terms of pollinator visit rates and diversity with direct effects on fruit and seed production, which is usually high, so pollen limitation on female fitness is not uncommon in this study system. However, pollen availability may show different levels between populations and years according to pollinator environment and selection through female function components is feasible to occur. Otherwise, the differential pollinator visitation on variation in flower size always translates into selection on larger flowers through male fitness. Despite this evidence, we propose that molecular analyses with genetic markers would be needed to record direct estimates of male reproductive success.
- (2) Floral production and maintenance costs are especially high in large flowers, especially in terms of water physiological use by transpiration under the hottest and driest conditions. Overall, these costs inherent to flower attractiveness and functional activity involve indirect costs in terms of fruit and seed production, which significantly increases in both larger-flowered individuals within-populations and larger-flowered species. Therefore, floral carbon and water costs limit female reproductive output and, consequently, exert abiotic negative

- selective pressures on flower size. It would be especially informative to study the relative importance of indirect costs as selective agents in relation to pollinators, especially between coflowering species with contrasting flower size.
- (3) Short floral longevity reported in the largest-flowered species *C. ladanifer* is in accordance with the elevated floral costs of this species. This pattern suggests that large-flowered plants blooming under hot and dry environments have to be short-lived, mediated by a fast fitness accrual rate, which involves an early and efficient pollination and a decrease in floral maintenance costs. Overall, this ephemeral floral longevity together with the high fruit and seed production, ecological context-dependent female pollen limitation and selection through maleness may keep the existence of large-flowered species in a Mediterranean environment.
 - (4) Lastly, larger flowers also entail costs in terms of florivory as are more likely attacked by antagonist insects, such as pollen- and petal-eater ants and beetles. Although we did not know the effects of this interaction on reproductive output and evolutionary consequences on flower size, florivores could readily exert relevant selective pressures on this trait, counteracting the positive effects of pollinators. It would be interesting to analyse this pattern as well as its relative importance in a multivariate fitness function estimating selection generated by pollinators and florivores on flower size through male and female function.

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