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New insights into plants coexistence in species-rich communities: the pollination interaction perspective

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Abstract

Questions: In animal-mediated pollination, pollinators can be regarded as a limiting resource for which entomophilous plant species might interact to assure pollination, an event pivotal for their reproduction and population maintenance. At community level, spatially aggregated co-flowering species can thus be expected to exhibit suitable suites of traits to avoid competition and ensure pollination. We explored the problem by answering the following questions: (i) are co-flowering species specialized on different guilds of pollinators? (ii) do co-flowering pollinator-sharing species segregate spatially? (iii) do co-flowering pollinator-sharing species that diverge in anther position spatially aggregate more than those that converge in anther position?

Study site: Euganean Hills (NE Italy).

Methods: Plant composition, flowering phenology and interactions between each entomophilous plant species and pollinating insects were monitored every fifteen days in 40 permanent plots placed in an area of 16 ha. We quantified the degree of flowering synchrony, pollinator-sharing and spatial aggregation between each pair of entomophilous species. We then tested the relationship between the degree of co-flowering, pollinator-sharing and spatial aggregation, and between spatial aggregation and anther position.

Results: Entomophilous species converged, at least partially in flowering time, and the phenological synchronization of flowering was significantly associated with the sharing of pollinator guilds. Co-flowering pollinator-sharing species segregated spatially. Furthermore, co-flowering pollinator-sharing species that diverged in anther position aggregated more than those that converged in anther position.

Conclusions: Reproductive traits that facilitate the coexistence of co-flowering species include specialization on different pollinator guilds and a phenological displacement of the flowering time. Furthermore, in circumstances of increased competition due to phenological synchronization, pollinator sharing and spatial aggregation, the chance of an effective pollination might depend on differences in anther position, resulting in a divergent pollen placement on pollinators' body. One of the most interesting results we obtained is that the presence of one mechanism does not preclude the operation of others and each plant species can simultaneously exhibit different strategies. Although

more studies are needed, our results can provide additional information about plant-plant interactions and add new insights into mechanisms allowing the coexistence of a high number of plant species into local communities.

Key words: Anther position; Assembly rules; Dry grasslands; Flowering synchrony; Pollinator-sharing; Spatial aggregation/segregation.

Nomenclature: Conti et al. 2005

Running head: Pollination interactions in plant communities.

Introduction

Temperate semi-natural dry grasslands are known for the high biodiversity they host. At small spatial scale, they stand out for the outstanding diversity in vascular plants (Purschke et al. 2012; Wilson et al. 2012; Wellstein et al. 2014). Beside plants, they provide the habitat for rare species from different taxonomic groups, including butterflies and other invertebrates (Van Helsdingen et al. 1996; Bobbink & Willems 1998; Ssymank et al. 1998; Van Swaay 2002; Fantinato et al. 2017).

Several studies attempted to pinpoint principles to explain the assembly of local communities and disentangle the complex and puzzling coexistence mechanisms that ensure the persistence of a high species richness. The essential question is how ecologically similar species can co-exist at small spatial scale. In classical community theory, plant community organization is typically assumed to be non-random (Gotelli & Graves 1996). According to the assembly rules hypothesis (Wilson & Gitay 1995; Wilson 1999; Götzenberger et al. 2012), patterns of species co-occurrence are driven by two main processes: a) habitat filtering, whereby species are selected according to their adaptation to environmental factors (Buffa & Villani 2012; Del Vecchio et al. 2015; 2016; Batalha et al. 2015; Pierce et al. 2017), and b) species interaction, with competition considered as a central factor in community assembly (Myers & Harms 2009; Kraft & Ackerly 2014), leading to nonrandom co-

occurrence patterns through niche differentiation or specialization (e.g., Tilman 1988; Pierce et al. 2007; Carboni et al. 2014; Kelemen et al. 2015).

Most studies of plant community assembly have focused on direct competitive interactions for space or nutrients (Sargent & Ackerly 2008; de Jager et al. 2011; Slaviero et al. 2016). However, interactions among plant species may arise during different stages in their life cycle, comprising both the vegetative growth phase, and reproduction, including pollination events and dispersion of seeds (Armbruster 1995; Hegland et al. 2009). Pollination is the first step of sexual reproduction, determining offspring (seeds) production and directly influencing the persistence of plant species into local communities (Ghazoul 2006; Callaway 2007; Dante et al. 2013).

In case of animal-mediated pollination, we can assume pollinators to be a limiting resource for which entomophilous plant species might interact among each other to assure pollination (Leonard et al. 2012). The most common pollination interactions that may occur are for pollinator attraction and heterospecific pollen transfer (e.g., Campbell & Motten 1985; Waser & Fugate 1986; Feinsinger 1987; Hegland & Totland 2005). Although case studies have revealed a range of possible outcomes (see Morales & Traveset 2008 for a review), from no detectable effect to strong fitness reduction, heterospecific pollen transfer can be regarded as a form of competition (McLernon et al. 1996; Muchhala et al. 2010; Ashman & Arceo-Gómez 2013) as it may change the amount and quality of the pollen dispersed between individuals of a given species (Mitchell et al. 2009), interfere with newly arriving legitimate pollen on the stigma and determine the loss of ovule receptivity to conspecific pollen (Brown & Mitchell 2001; De Jong 2012), resulting in pollen loss and negative effects on interacting species. Particularly, in plant communities heterospecific pollen transfer is extremely common (Fang & Huang 2013) and its fitness costs are assumed to guide the expression of morphological, phenological and physiological traits aimed to reduce them (Muchhala et al. 2010; Ashman & Arceo-Gómez 2013; Lázaro et al. 2015).

Interactions for pollinator attraction, which influence the number of flower visits a plant receives (Mitchell et al. 2009), can span from competition to facilitation, as extremes of a continuum (Lázaro et al. 2009; 2014).

Plants may compete for pollinators if a plant species draws away effective visitors from another species, thus limiting its reproductive success (Pleasants 1980; Mitchell et al. 2009; van der Kooi et al. 2016). However, also a mutually beneficial pollinator attraction strategy may occur, based on increased floral visitation due to larger floral displays and resource availability and complementation (Podolsky 1992; Ghazoul 2006; Jakobsson & Ågren 2014).

Since pollinators tend to visit nearby plant species, spatially aggregated co-flowering species are likely to experience stronger competition for pollinators and potentially suffer higher pollen loss and fitness decrease due to heterospecific pollen transfer (Fang & Huang 2013; van der Kooi et al. 2016). Adaptations to minimize competition and pollen loss may include all those changes that reduce the sharing of pollinators such as specialization on different pollinators (Muchhala et al. 2010; Kipling & Warren 2014; Ruchisansakun et al. 2016); shifts in flowering time (Gleeson 1981; Devaux & Lande 2009); a segregate spatial distribution (Mosquin 1971; Pleasants 1980; Kipling & Warren 2014); or divergence in floral traits such as the anther position, which allows pollinator-sharing species to avoid pollen loss by placing pollen on different parts of pollinators bodies (Ruchisansakun et al. 2016).

In a previous study, Fantinato et al. (2016a) proved that in temperate dry grasslands, as in all the biomes, animal-pollinated plant species overlap in flowering time mostly due to climatic constraints. Co-flowering species have been widely recognized to share pollinators, suggesting that competition for pollination might be a widespread phenomenon in many terrestrial ecosystems (Waser et al. 1996; Moeller 2004; Cozzolino et al. 2005). Given the high degree of co-flowering and thus a highly expected pollinator-sharing in dry grasslands, we can expect that spatially aggregated co-flowering species exhibit suitable suites of reproductive traits which may concur to minimize competition for pollination and pollen loss due to heterospecific pollen transfer thereby assuring a steady co-existence of a high number of animal-pollinated species.

In light of these considerations we addressed the problem by answering the following questions: (i) are co-flowering species specialized for different guilds of pollinators? (ii) do co-flowering species sharing pollinators segregate spatially? (iii) do co-flowering pollinator-sharing species that diverge in anther position spatially aggregate more than those that converge in anther position?

Material and methods

Study area

Field sampling was carried out on semi-natural, oligo- to mesotrophic, *Bromus erectus* dominated dry grasslands in the Euganean Hills (NE Italy). The investigated dry grasslands can be included in the class *Festuco-Brometea* Br.-Bl. & Tx. ex Soó 1947 and the SE-European-Illyrian order *Scorzoneretalia villosae* Kovačević 1959 (= *Scorzonero-Chrysopogonetalia* Horvatić & Horvat In Horvatić 1963; Fantinato et al. 2016b; Mucina et al. 2016). In the study area, dry grasslands cover a total surface of about 16 ha and establish on middle-altitude limestone slopes (average altitude 100 m a.s.l.), on sites characterised by poorly developed, shallow and skeletal calcareous soils, with a very low water availability (AWC), and average pH of 7.5 (Bini 2001; Fantinato et al. 2016b). Once managed by low-intensive mowing practices, since 1980s dry grasslands have experienced increasing abandonment. From 2003 they are subject to mowing every three years.

Data collection

We randomly placed 40 permanent plots of 2 m x 2 m. To reduce spatial autocorrelation the minimum distance between plots was set at 25 m (Vaz et al. 2015). In each plot, vascular species composition was recorded and flowering phenology of all entomophilous species (35 species; Appendix S1) was monitored every fifteen days (1st April to 12th September in 2016) for a total of 11 surveys. Flowering was considered started when the first flower was observed to be open on an individual plant (Pleasants 1980) and ended when individual plants no longer possessed any flower with anthers (Dante et al. 2013).

Further, during each survey, in 20 out of the 40 permanent plots we also recorded visiting insects, under warm and sunny weather conditions. The visitation frequency was monitored by counting the number of visits to each plant species over 15 minutes. The observation period was split in 5-min sets distributed during three daily intervals (from 10 a.m. to 12 a.m.; from 12 a.m. to 2 p.m.; from 2 p.m. to 4 p.m.). We considered and counted as pollinators only those insects landing on the flower, visiting it for more than 1 s, and getting in direct contact with the floral reproductive organs (Hegland & Totland 2005).

Furthermore, for the 35 entomophilous plant species we recorded anther position relative to the corolla. Accordingly, plant species were grouped into three categories: plant species with anthers exerting from the bottom of the corolla (e.g., in *Geranium sanguineum*, *Scabiosa triandra* and *Ononis natrix*); plant species with anthers exerting from the top of the corolla (e.g., in *Melampyrum barbatum*, *Stachys recta* and *Thymus pulegioides*); and plant species with anthers inserted nearby the opening of the corolla tube (e.g., in *Campanula rapunculus*, *Muscari comosum* and *Orchis simia*).

Anther position can be interpreted as a subtle mechanism to reduce pollen loss due to heterospecific pollen transfer as it leads to differences in pollen placement on pollinator's body (Ruchisansakun et al. 2016). Hence, in the first group plant species place pollen mostly on the legs and on the ventral side of the insect body, in the second group mostly on the dorsal side, while in the third group in the correspondence of the head (e.g., Westerkamp et al. 2007; Schiestl & Schlüter 2009).

Pollinators were identified to species or genus (morphospecies) and then grouped into 11 guilds which allow to analyze pollination interactions from the perspective of function rather than of species identity (e.g., Fang & Huang 2013; Fontaine et al. 2006), thus revealing patterns in the functionality in pollination interactions: small solitary bees, large solitary bees, medium social bees, large social bees, beetles, syrphid flies, other flies, butterflies, wasps, ants, and bush-crickets. In accordance with previous studies (Fenster et al. 2004; Moretti et al. 2009; Koski et al. 2015; Arceo-Gomez et al. 2015), guilds are based on the visitor's morphology (e.g., body size), energetic requirements, flight ability and foraging/feeding behavior, which can determine the range of flowers they can visit and thus the type of selection they generate. Members of a given guild are thus more similar to each other than to members of other groups (Geslin et al. 2013; Rosas-Guerrero et al. 2014; Koski et al. 2015). Bush-crickets have been included as a pollinator guild because juveniles were observed to land on flowers and to carry pollen accidentally on their legs and make contact with the floral reproductive organs.

Data analysis

Plant flowering synchronization and spatial assemblage

To quantify the overlap in the flowering time between each pair of plant species we used the Co-Flowering index (CF-index; Fantinato et al. 2016a). We created a presence-absence matrix (flowering matrix), where rows were species (35 entomophilous species) and columns were the 11 surveys.

Entries represented the presence (1) or the absence (0) of the flowering event. We then calculated the CF-index through Pearson's correlation. The value of the CF-index is equivalent to the value of the Pearson's correlation coefficient between the presence/absence vectors of two species and can range from -1 (i.e. complete flowering asynchrony) to $+1$ (i.e. complete flowering synchrony; Fantinato et al. 2016a). Results were organized in a symmetric matrix (species x species; hereafter CF matrix).

We performed the same procedure to quantify the spatial association of each pair of species. In this case, we used a species x plot matrix (35 entomophilous species x 40 plots), where entries represented the presence (1) or the absence (0) of a species in a plot. For each pair of species we calculated the V-score (Lepš & Šmilauer 2003) through Pearson's correlation. The values range from $+1$ (complete spatial association) to -1 (complete spatial segregation). We obtained a symmetric matrix (species x species; hereafter V matrix).

Pollinator-sharing

To quantify the degree to which pairs of plant species share pollinator guilds, we created an abundance matrix where rows were plant species (35 plant species), and columns were insect guilds (11 guilds). In this case, entries represented the number of contacts observed between plants and insects belonging to a given pollinator guild, calculated as the sum of all the contacts recorded in each monitored plot through the entire flowering season. We chose to use abundance data instead of presence-absence data, because abundances allow to distinguish frequent visits from occasional contacts. For each pair of plant species we compared the abundance of pollinator guilds via Spearman's rank correlation. Spearman's rank correlation was chosen because it provides a reliable comparison of plant species pollinators irrespectively of any form of standardization (e.g., for the total number of flowers per species or for the total number of visits).

The values of r_s indicate the trend of a pair of species to share pollinators. A positive correlation coefficient ($r_s \sim 1$) indicates that two plant species share the same guilds of pollinators, while a negative correlation coefficient ($r_s \sim -1$) represents the case in which plant species do not share pollinator guilds. The Spearman's values were organized in a symmetric matrix (PS matrix; namely Pollinator-Sharing matrix) of plant species.

Co-flowering species, pollinator-sharing and spatial assemblage

To assess whether co-flowering species are sharing or not pollinators, and whether plant species that co-flower (CF-index > 0) and share pollinator guilds ($r_s > 0$) are spatially aggregated or segregated, we applied a series of Mantel tests (function "mantel" in the R-based package "Vegan"). Specifically, we correlated the CF matrix with the PS matrix; then we correlated the CF matrix with the V matrix by selecting only pairs of species that co-flowered and shared pollinator guilds. The significance of the correlation matrix was assessed by comparing observed values of the Mantel statistic to a random distribution generated through 999 permutations of the rows and columns (Legendre & Legendre 2012).

A positive and significant correlation between the CF matrix and the PS matrix would indicate that co-flowering plant species share pollinator guilds, while a negative value of the Mantel's r would indicate that co-flowering plant species are visited by different guilds of pollinators. A positive and significant correlation between the CF matrix and the V matrix would indicate that co-flowering species are spatially aggregated, while a negative and significant correlation would indicate spatial segregation.

Anthers position

For each pair of co-flowering pollinator-sharing species (i.e., CF-index and $r_s > 0$) we tested if anther position differed more between spatially aggregated (V-score > 0) plant species than between spatially segregated (V-score < 0) plant species. Especially, we assigned 1 to all pairs of plant species in which anther position coincided and 0 to those in which anther position differed. Significant differences were detected by performing a non-parametric Mann-Whitney U-Test. We used spatially aggregated

(V-score > 0) vs. spatially segregated (V-score < 0) plant species as grouping variable and the coincidence (1) or the difference (0) in anther position as dependent variable.

All calculations performed in the present study were done within the R statistical framework (R-Development-Core-Team 2012).

Results

Animal-pollinated species converged in flowering time, with 66.2% of species pairs overlapping, at least partially, in their flowering time (394 species pairs; CF-index > 0). Overall, 91 species pairs (15.3%) strongly overlapped in flowering time (CF > 0.75), while 115 species pairs (19.3%) showed a moderate overlap (0.75 > CF > 0.50). 201 species pairs (33.8%) showed temporal separation (CF-index < 0), with 10 pairs of species (1.7%) with a strong phenological displacement of flowering (CF-index < -0.75).

The phenological synchronization of flowering was significantly associated with the sharing of pollinator guilds (Mantel test: CF matrix vs. PS matrix; $P = 0.001$; $r = 0.13$; Fig. 1). Overall, 38.5% of species pairs (229 pairs) showed synchronous flowering periods coupled with pollinator-sharing (CF-index > 0 and $r_s > 0$), while 27.7% of species pairs (165 pairs), although flowering synchronously (CF-index > 0), relied pollination on different guilds of pollinators ($r_s < 0$). 19.5% of species pairs (116 pairs) segregated temporally (CF-index < 0) but relied upon the same guilds of pollinators ($r_s > 0$).

Pairs of co-flowering pollinator-sharing species (i.e., CF-index > 0 and $r_s > 0$) disclosed a significant negative correlation between the degree of co-flowering and the spatial aggregation (Mantel test: CF matrix vs. V matrix; $P = 0.036$; $r = -0.14$; Fig. 2), namely, the higher the flowering synchrony, the lower the spatial aggregation. In particular, 104 species pairs (17.5%) spatially aggregated (V-score > 0), while 125 species pairs (21.0%) segregated (V-score < 0). All pollinator-sharing plant species that showed a complete flowering synchrony (CF-index = 1; 11 species pairs; i.e., 1.8%), were spatially segregated (i.e., $r_s > 0$; CF = 1; V-score < 0).

Anther position of co-flowering pollinator-sharing species (i.e., CF-index and $r_s > 0$) significantly differed between spatially aggregated (V-score > 0) and segregated (V-score < 0) species, with spatially aggregated species differing in anther position more frequently than spatially segregated species (Mann-Whitney; $Z = -3.18$; $P < 0.01$).

Discussion

Our results demonstrated that in dry grasslands, entomophilous plant species exhibit different strategies to reduce competition and pollen loss thereby assuring pollination, a pivotal event for reproduction, offspring production and population maintenance into local communities.

Temperate dry grassland entomophilous species revealed a non-random pattern of flowering with a high degree of convergence in the timing of flower. In seasonal climates, like in temperate and Mediterranean climates, insect-pollinated plants are forced to flower during periods when climatic conditions are most suitable for reproduction (e.g., time available for flowering and seed maturation) (Elzinga et al. 2007) and generally match with the most favorable season for pollinator activity.

The flowering synchrony turned out to be positively correlated to the sharing of pollinator guilds, a result in line with those of other studies (e.g., Motten 1986; Cozzolino et al. 2005) stating that pollinator-sharing is a widespread phenomenon.

It has been argued that the convergence of flowering phenology among plant species in a community may function as a pollinator-mediated facilitation through the improvement of pollinator attraction due to mass flowering (Aizen & Vázquez 2006; Sargent & Ackerly 2008), or increased diversity (Ghazoul 2006). The convergence of flowering periods over the spring months enables the plant community to support a wide range of visitors (Potts et al. 2003), by increasing floral resources availability and heterogeneity (e.g., nectar and pollen), which assure the maintenance of pollinators seeking single or multiple resources (Ebeling et al. 2008). However, our results indicated that a notable amount of co-flowering species pairs (27.7%) were specialized to attract different pollinator guilds. Community context and strong interactions with competitors have been already recognized as forces promoting specialization on different pollinators (Jakobsson et al. 2009; Muchhala et al. 2010). Arguably, despite the positive effects that it can have on pollinator attraction, pollinator-sharing by

co-flowering species may increase competition for pollinators as well as heterospecific pollen transfer (Price 1984; Potts et al. 2003; Carvalheiro et al. 2014), which may result in negative effects on plant species reproduction (Morales & Traveset 2008). Co-flowering plant species may compete with each other for pollinator services thereby affecting each other's pollinator visits (Lázaro et al. 2009) and many studies on co-flowering pollinator-sharing species demonstrated increased competition and reduced pollination rate during periods of flowering overlap (Morales & Traveset 2008; van der Kooi et al. 2016). The positive outcome of specialization becomes clear when considering that plants produce a finite quantity of pollen and selection will favor maximizing the number of grains that reach conspecific stigmas (Harder & Routley 2006).

Besides specialization on different pollinators, dry grassland entomophilous species also showed patterns of temporal segregation, namely a shift in the flowering period. It has been already suggested (Aizen & Vázquez 2006) that competition for pollination may cause evolutionary displacement or ecological sorting of flowering phenologies. Being normally in low number, early or late flowering species are expected to have fewer competitors in their neighborhood than are plants flowering at or near the peak of the community (Elzinga et al. 2007). In our case, despite the overriding influence of climate, a non-negligible amount of species pairs (33.8%) showed a modulation of the flowering time, thus reducing competition by blooming at different times. This result becomes even more interesting when considering that 19.5% of species pairs which segregate temporally shared pollinators. Thus, the phenological displacement of flowering allows species to rely on the same resource for pollination without incurring strong competition, and to maintain the community of pollinators for a longer period of time (Willmer 2011).

However, Vamosi et al. (2006) suggested that in competitive environments specialization on different pollinators or the displacement of the flowering period may be insufficient to reduce competition.

Despite a relative low Mantel correlation coefficient, we disclosed a significant negative correlation between the degree of co-flowering and the spatial aggregation. Especially, in dry grassland communities, all those species which evidenced a complete flowering synchrony (CF-index = 1) and shared pollinator guilds ($r_s > 0$), displayed a striking pattern which involved a spatial segregation (V-score < 0). Thus, although plant species substantially overlap in flowering time and rely on the same

pollinator guild, they are separated in space. Spatial proximity has been shown to possibly affect the intensity of pollination experienced by a given plant (Thomson 1978; Hegland & Totland 2005; Törang et al. 2007; Hersch & Roy 2007). Lázaro et al. (2009) demonstrated that both the diversity and the composition of pollinators of particular plant species are affected not only by the characteristics of the individual plant species itself and its abundance but also by the identity, diversity and density of the co-flowering neighbor plants. Therefore, we can hypothesize that at small-scale the pollination success of plant species, and consequently their reproductive fitness, might increase when individuals are segregated from competitors (Jakobsson et al. 2009; Lázaro et al. 2014). A spatial patchiness of co-flowering pollinator-sharing species may therefore increase the proportion of intra-specific visits made by pollinators, ultimately reducing the chance that where co-flowering pollinator-sharing species co-occur at small spatial scale, either of them would be excluded from the community. However, further studies on plant fitness would be needed to test our hypothesis and prove that spatially segregated plant species increase their reproductive success.

A certain amount of species pairs (17.5%) co-flowered, shared pollinator guilds and were spatially aggregated. This particular situation is expected to increase competition for pollinator attraction as well as pollen loss due to heterospecific pollen transfer (Lázaro et al. 2009; Fang & Huang 2013). In this regard, it is particularly interesting to observe that, in dry grasslands, spatially aggregated plant species diverged in anther position more frequently than spatially segregated species, so that a shared pollinator would get pollen on different parts of its body. Flowers with a similar sexual architecture are expected to be particularly likely to exchange pollen due to the increasing overlap in pollinator species and the load of pollen on the same parts of pollinators' body (Montgomery & Rathcke 2012). Since pollen deposition is related to the placement of pollen on the body of flower visitors, a different anther position mechanically allows species to benefit from living in close proximity and sharing pollinators, while, at the same time, minimizing reproductive interference and pollen loss due to heterospecific pollen transfer (Caruso 1999; Morales & Traveset 2008). Additionally, floral similarity may also decrease pollinator constancy (Waser 1986). Thus, differences in anther position among spatially aggregated, co-flowering pollinator-sharing species can be regarded as a way to avoid reproductive interference, particularly in circumstances where climatic constraints allow little

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opportunity for displacement in floral phenology. Several examples of differential pollen placement for congener plant species have been provided (Sprague 1962; Muchhala & Potts 2007; Smith & Rausher 2008). Further evidence was also found between taxonomically distinct flowers (Goldbatt et al. 1995), yet patterns of pollen placement diversification at community level have so far received less attention (but see Armbruster et al. 1994).

Conclusions

Plant-pollinator interactions are essential for outcrossing in most flowering plant species, thereby influencing offspring production and in turn the long-lasting permanence of plant species in the community. Although some correlations we found were weak and need to be supported by further research, our study confirms that pollination interactions contribute to shape patterns of species coexistence by selecting those species which exhibit suitable suites of reproductive traits that are supposed to reduce competition. When establishing in a species-rich plant community, the pollination success of a plant species depends on differences between its own phenological and morphological features and those of the co-occurring species. Reproductive traits that facilitate the coexistence of co-flowering species include specialization on different pollinator guilds and a phenological displacement of the flowering time.

Furthermore, in circumstances of increased competition due to phenological synchronization, pollinator sharing and spatial aggregation, the chance of an effective pollination might depend on differences in anther position, resulting in a divergent pollen placement on pollinators' body, a way to utilize the same insects as pollinators without incurring significant loss of pollen.

The low Mantel's coefficients we obtained might just be due to the fact that there isn't a dominant mechanism, rather each plant species can simultaneously exhibit different strategies. One of the most interesting results we obtained is that the presence of one mechanism does not preclude the operation of others. Although more studies are needed, our results can provide additional information about plant-plant interactions and add new insights into mechanisms allowing the coexistence of a high number of plant species into local communities.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of entomophilous species recorded in the studied dry grasslands. For each animal pollinated plant species we provide the flowering time and the percentage of each visiting pollinator guild calculated on the number of visits recorded.

Figure captions

Fig. 1. Scatterplot of co-flowering values (CF-index values) versus pollinator sharing values (Spearman's coefficients) calculated through Mantel test ($P = 0.001$; $r = 0.13$). Empty dots represent pairs of co-flowering species that share pollinator guilds; empty rhombus pairs of species with disjointed flowering periods but sharing pollinator guilds; empty squares pairs of species with disjointed flowering periods visited by different guilds of pollinator; empty triangles pairs of co-flowering species visited by different guilds of pollinators.

Fig. 2. Scatterplot of co-flowering values (CF-index values) versus co-occurrence values (V-score values) of pairs of species proven to flower synchronously ($CF\text{-index} > 0$) and to share pollinator guilds ($r_s > 0$) calculated through Mantel test ($P = 0.036$; $r = -0.14$).



