


New insights into plants co-existence 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: (1) are co-flowering species specialized on different guilds of pollinators; (2) do co-flowering pollinator-sharing species segregate spatially; and (3) 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 15 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 co-existence 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 effective pollination might depend on differences in anther position, resulting in a divergent pollen placement on pollinator bodies. 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 provide new insights into mechanisms allowing the co-existence of a high number of plant species in local communities.

KEYWORDS

anther position, assembly rules, dry grasslands, flowering synchrony, pollinator-sharing, spatial aggregation/segregation

1 | 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 of vascular plants (Purschke, Sykes, Reitalu, Poschlod, & Prentice, 2012; Wellstein et al., 2014; Wilson, Peet, Dengler, & Pärtel, 2012). Beside plants, they provide habitat for rare species from different taxonomic groups, including butterflies and other invertebrates (Bobbink & Willems, 1988; Fantinato, Del Vecchio, Baltieri, Fabris, & Buffa, 2017; Szymank, Hauke, Rückriem, & Schröder, 1998; Van Helsing, Willemse, & Speight, 1996; Van Swaay, 2002).

Several studies have attempted to pinpoint principles to explain the assembly of local communities and disentangle the complex and puzzling co-existence mechanisms that ensure the persistence of a high species richness. The essential question is how ecologically similar species can co-exist at small spatial scales. In classical community theory, plant community organization is typically assumed to be non-random (Gotelli & Graves, 1996). According to the assembly rules hypothesis (Götzenberger et al., 2012; Wilson, 1999; Wilson & Gitay, 1995), 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 (Batalha, Pipenbahr, Bakan, Kaligarič, & Škornik, 2015; Buffa & Villani, 2012; Del Vecchio, Pizzo, & Buffa, 2015; Del Vecchio, Slaviero, Fantinato, & Buffa, 2016; Pierce et al., 2017), and (b) species interaction, with competition considered as a central factor in community assembly (Kraft & Ackerly, 2014; Myers & Harms, 2009), leading to non-random co-occurrence patterns through niche differentiation or specialization (e.g. Carboni et al., 2014; Kelemen et al., 2015; Pierce, Luzzaro, Caccianiga, Ceriani, & Cerabolini, 2007; Tilman, 1988).

Most studies of plant community assembly have focused on direct competitive interactions for space or nutrients (de Jager, Dreyer, & Ellis, 2011; Sargent & Ackerly, 2008; Slaviero, Del Vecchio, Pierce, Fantinato, & Buffa, 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 dispersal of seeds (Armbruster, 1995; Hegland, Grytnes, & Totland, 2009). Pollination is the first step of sexual reproduction, determining offspring (seeds) production and directly influencing the persistence of plant species in local communities (Callaway, 2007; Dante, Schamp, & Aarssen, 2013; Ghazoul, 2006).

In the case of animal-mediated pollination, we can assume pollinators are a limiting resource for which entomophilous plant species might interact with each other to assure pollination (Leonard,

Dornhaus, & Papaj, 2012). The most common pollination interactions that can occur are for pollinator attraction and heterospecific pollen transfer (e.g. Campbell & Motten, 1985; Feinsinger, 1987; Hegland & Totland, 2005; Waser & Fugate, 1986). 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 (Ashman & Arceo-Gómez, 2013; McLernon, Murphy, & Aarssen, 1996; Muchhala, Brown, Armbruster, & Potts, 2010) as it may change the amount and quality of the pollen dispersed between individuals of a given species (Mitchell, Flanagan, Brown, Waser, & Karron, 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. In particular, 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 at reducing them (Ashman & Arceo-Gómez, 2013; Lázaro, Lundgren, & Totland, 2015; Muchhala et al., 2010). 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, Lundgren, & Totland, 2009, 2014). Plants may compete for pollinators if a plant species draws away effective visitors from another species, thus limiting its reproductive success (van der Kooij, Pen, Staal, Stavenga, & Elzenga, 2016; Mitchell et al., 2009; Pleasants, 1980). However, also a mutually beneficial pollinator attraction strategy may occur, based on increased floral visitation due to larger floral displays, resource availability and complementation (Ghazoul, 2006; Jakobsson & Ågren, 2014; Podolsky, 1992).

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 Kooij 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 (Kipling & Warren, 2014; Muchhala et al., 2010; Ruchisansakun, Tangtorwongsakul, Cozien, Smets, & van der Niet, 2016), shifts in flowering time (Devaux & Lande, 2009; Gleeson, 1981), a segregated spatial distribution (Kipling & Warren, 2014; Mosquin, 1971; Pleasants, 1980); 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, Del Vecchio, et al. (2016) 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 (Cozzolino et al., 2005; Moeller, 2004; Waser, Chittka, Price, & Williams, 1996). Given the high degree of co-flowering and thus generally expected pollinator-sharing in dry grasslands, we can expect that spatially aggregated co-flowering species exhibit suitable suites of reproductive traits that may concur to minimize competition for pollination and pollen loss due to heterospecific pollen transfer, thereby assuring steady co-existence of a high number of animal-pollinated species. In light of these considerations we addressed the problem through the following questions: (1) are co-flowering species specialized for different guilds of pollinators; (2) do co-flowering species sharing pollinators segregate spatially; and (3) do co-flowering pollinator-sharing species that diverge in anther position spatially aggregate more than those that converge in anther position?

2 | METHODS

2.1 | 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-Illlyrian order *Scorzoneretalia villosae* Kovačević 1959 (= *Scorzonero-Chrysopogonetalia* Horvatić & Horvat In Horvatić 1963; Fantinato, Giovanetti, Del Vecchio, & Buffa, 2016; 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 characterized by poorly developed, shallow and skeletal calcareous soils, with very low water availability (AWC) and average pH of 7.5 (Bini, 2001; Fantinato, Giovanetti, et al., 2016). Once managed by low-intensive mowing practices, since the 1980s dry grasslands have experienced increasing abandonment. From 2003 onwards they have been mowed every 3 years.

2.2 | Data collection

We randomly placed 40 permanent plots of 2 m × 2 m. To reduce spatial autocorrelation, the minimum distance between plots was set at 25 m (Vaz, Macedo, Alves, Honrado, & Lomba, 2015). In each plot, vascular species composition was recorded and flowering phenology of all entomophilous species (35 species; Appendix S1) was monitored every 15 days (1 April to 12 September 2016) for a total of 11 surveys. Flowering was considered to have begun 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 through counting the number of visits to each plant species over 15 min. The observation period was split in 5-min sets distributed over three daily intervals (from 10:00 hr to 12:00 hr; from 12:00 hr to 14:00 hr; from 14:00 hr to 16:00 hr). We considered and counted as pollinators only those insects landing on the flower, visiting it for more than 1 s, and being 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. *Geranium sanguineum*, *Scabiosa triandra* and *Ononis natrix*); plant species with anthers exerting from the top of the corolla (e.g. *Melampyrum barbatum*, *Stachys recta* and *Thymus pulegioides*); and plant species with anthers inserted near the opening of the corolla tube (e.g. *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 a 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 close to the head (e.g. Schiestl & Schlüter, 2009; Westerkamp & Claßen-Bockhoff, 2007).

Pollinators were identified to species or genus (morphospecies) and then grouped into 11 guilds, which allows analysis of pollination interactions from the perspective of function rather than of species identity (e.g. Fang & Huang, 2013; Fontaine, Dajoz, Meriguet, & Loreau, 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-cricket. In accordance with previous studies (Arceo-Gomez et al., 2015; Fenster, Armbruster, Wilson, Dudash, & Thomson, 2004; Koski et al., 2015; Moretti, De Bello, Roberts, & Potts, 2009), guilds are based on the visitor's morphology (e.g. body size), energy requirements, flight ability and foraging/feeding behaviour, 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, Gauzens, Thébault, & Dajoz, 2013; Koski et al., 2015; Rosas-Guerrero et al., 2014). Bush-cricket 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.

2.3 | Data analysis

2.3.1 | 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, Del

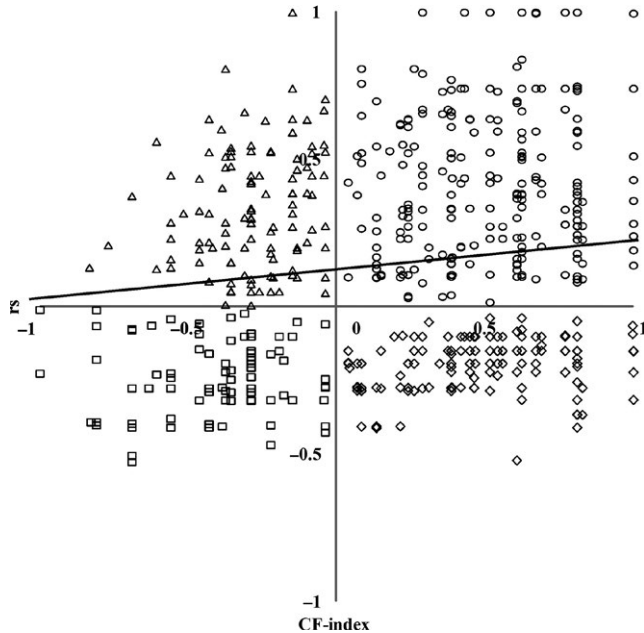


FIGURE 1 Scatterplot of co-flowering values (CF index values) vs. pollinator-sharing values (Spearman's coefficients) calculated through Mantel tests ($p = .001$, $r = .13$). Empty dots represent pairs of co-flowering species that share pollinator guilds; empty rhombus – pairs of species with disjointed 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 pollinator

Vecchio, et al., 2016). 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, Del Vecchio, et al., 2016). Results were organized in a symmetric matrix (species \times 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 \times plot matrix (35 entomophilous species \times 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 \times species; hereafter V matrix).

2.3.2 | 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 throughout the entire flowering season. We chose to use abundance data instead of presence–absence data, because abundances allow us 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 irrespective 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.

2.3.3 | Co-flowering species, pollinator-sharing and spatial assemblage

To assess whether co-flowering species are or are not sharing 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”; R Foundation for Statistical Computing, Vienna, Austria). 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.

2.3.4 | Anther 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. In particular, 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.

3 | 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 ($0.75 > \text{CF} > 0.50$). A total of 201 species pairs (33.8%) showed temporal separation (CF index < 0), with ten 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; $p = .001$, $r = .13$; Figure 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 on pollination from different guilds of pollinators ($r_s < 0$). About 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; $p = .036$, $r = -.14$; Figure 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 $Z = -3.18$, $p < .01$).

4 | 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 flowering. In seasonal climates, as 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 the most favourable season for pollinator

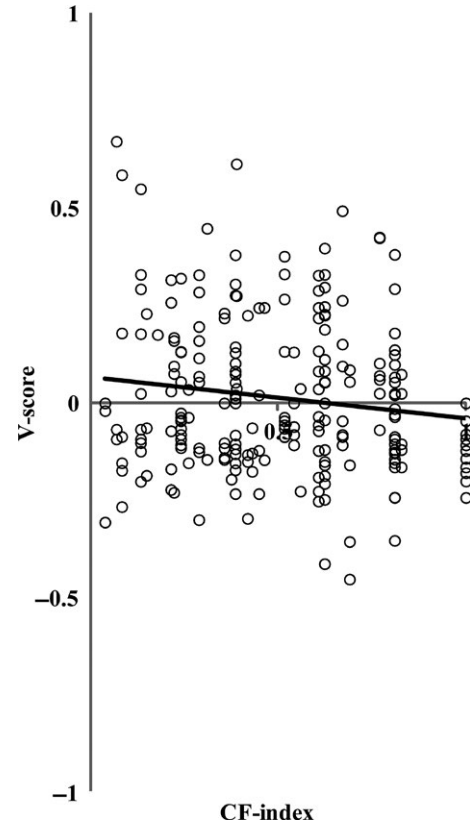


FIGURE 2 Scatterplot of co-flowering values (CF index values) vs. co-occurrence values (V score values) of pairs of species proven to flower synchronously (CF index > 0) and to share pollinator guilds ($r_s > 0$) calculated through Mantel tests ($p = .036$, $r = -.14$)

activity. The flowering synchrony was positively correlated to the sharing of pollinator guilds, a result in line with those of other studies (e.g. Cozzolino et al., 2005; Motten, 1986) 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 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, Vulliamy, Dafni, Ne, & Willmer, 2003), by increasing floral resource availability and heterogeneity (e.g. nectar and pollen), which assure the maintenance of pollinators seeking single or multiple resources (Ebeling, Klein, Schumacher, Weisser, & Tscharntke, 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 already been recognized as forces promoting specialization on different pollinators (Jakobsson, Lázaro, & Totland, 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 (Carvalho et al., 2014; Potts et al., 2003; Price, 1984), 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 others 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 (van der Kooi et al., 2016; Morales & Traveset, 2008). The positive outcome of specialization becomes clear when considering that plants produce a finite quantity of pollen and selection will favour 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 already been suggested (Aizen & Vázquez, 2006) that competition for pollination may cause evolutionary displacement or ecological sorting of flowering phenologies. Being normally at low numbers, early or late flowering species are expected to have fewer competitors in their neighbourhood 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 modulation of flowering time, thus reducing competition by blooming at different times. This result becomes even more interesting when considering that 19.5% of species pairs that 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 found a significant negative correlation between the degree of co-flowering and the spatial aggregation. Especially in dry grassland communities, all those species that evidenced complete flowering synchrony (CF index = 1) and shared pollinator guilds ($r_s > 0$), displayed a striking pattern that involved 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 (Hegland & Totland, 2005; Hersch & Roy, 2007; Thomson, 1978; Törang, Ehrlén, & Agren, 2006). 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 neighbour plants. Therefore, we can hypothesize that at small scales 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 intraspecific visits made by pollinators, ultimately reducing the chance that where co-flowering pollinator-sharing species co-occur at small spatial scales, 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.

Some 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 (Fang & Huang, 2013; Lázaro et al., 2009). 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 obtain 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 pollinator's 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 opportunity for displacement in floral phenology. Several examples of differential pollen placement for congener plant species have been provided (Muchhala & Potts, 2007; Smith & Rausher, 2008; Sprague, 1962). Further evidence was also found between taxonomically distinct flowers (Goldblatt, Manning, & Bernhardt, 1995), yet patterns of pollen placement diversification at community level have so far received less attention (but see Armbruster, Edwards, & Debevec, 1994).

5 | CONCLUSIONS

Plant-pollinator interactions are essential for outcrossing in most flowering plant species, thereby influencing offspring production and in turn the long-term 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 co-existence by selecting those species that exhibit suitable suites of reproductive traits that are considered 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 co-existence of co-flowering species include specialization on different pollinator guilds and phenological displacement of the flowering time. Furthermore, in circumstances of increased competition due to phenological synchronization, pollinator-sharing and spatial aggregation, the chance of effective pollination might depend on

differences in anther position, resulting in divergent pollen placement on a pollinator's body, a method to utilize the same insects as pollinators without incurring significant loss of pollen.

The low Mantel coefficients we obtained might just be due to the fact that there is no 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 provide additional information about plant–plant interactions and add new insights into mechanisms allowing the co-existence of a high number of plant species in local communities.

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SUPPORTING INFORMATION

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

APPENDIX S1 List of entomophilous species recorded in the studied dry grasslands

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