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## Animal-mediated interactions for pollination in saltmarsh communities

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### Abstract

Among the wide variety of biotic interactions, animal-mediated pollination plays a crucial role in the maintenance of the integrity of plant communities. Thus, there is increasing concern about the possible effects that the growing loss of pollinators (i.e., pollinator crisis phenomenon) might have on plant communities. Recent studies revealed that pollination interactions often occur at the landscape scale, with plant species of different communities interacting through pollinator sharing. Saltmarshes provide a suitable example of plant communities spatially co-occurring at the landscape scale, with the micro-topography determining a precise zonation of ecologically distinct halophytic communities. However, little is still known about pollination interactions in saltmarshes. The aim of the present study was to assess which halophytic community contribute best to pollinator species richness in saltmarshes and whether plant species of different halophytic communities interact through pollinator sharing. To this aim we placed 20 permanent plots per plant community and monitored pollination interactions between plants and pollinators once a month during the overall flowering season. Our results revealed that animal-mediated pollination occurred in only two halophytic communities, with three species depending on animals for their pollination. When comparing halophytic communities in terms of richness of pollinator species, the vegetation of sandbanks, mudflats and sandflats emerged as the richest one. Animal-pollinated species of saltmarshes only partially shared pollinator species, revealing an overall low exchange of pollinators between different halophytic communities. In conclusion, the high complementarity in the spectrum of pollinators showed by animal-pollinated species of different halophytic communities makes all halophytic communities hosting animal-pollinated species important for the conservation of pollinators.

Key words: Biodiversity conservation, biotic interactions, halophytic communities, landscape, pollinators, Venice lagoon.

### Introduction

Among the wide variety of biotic interactions, animal-mediated pollination plays a crucial role in the maintenance of the integrity of plant communities (Fantinato *et al.*, 2019a). Nearly 4 out of 5 of both wild plants and crops depend on animal-pollination, often provided by wild, unmanaged, pollinator species (Klein *et al.*, 2007; Winfree, 2008). Moreover, in natural and semi-natural plant communities, pollination-related interactions remarkably contribute to shaping patterns of plant species distribution and co-occurrence (Pellissier *et al.*, 2010; Heystek & Pauw, 2014; Fantinato *et al.*, 2018a).

Given the importance of animal-mediated pollination for the integrity of plant communities, there is increasing concern about the growing loss of pollinator species (Potts *et al.*, 2010). According to the IPBES (2016), over 40% of invertebrate pollinators are at risk of extinction, mostly bees and butterflies. Pollinator decline is expected to limit not only wild plants reproduction, but also crop production, thereby threatening food security for humans and wildlife as well as global economic stability (Burkle *et al.*, 2013; Garibaldi *et al.*, 2013; Tylianakis, 2013). Although pollinator

populations are affected by a range of factors, such as increasing use of agrochemicals, parasites and diseases, local and global environmental degradation and the loss of flowering plants in natural and semi-natural communities are ranked at the top of threatening factors in determining their decline (Kosior *et al.*, 2007).

During the last decades, the need to forecast the possible effects of pollinator decline on plant communities has stimulated studies to deepen our understanding of the role of animal-mediated pollination in assuring the integrity of natural and semi-natural communities. So far, the focus has been on a few communities outstanding for their high species richness (Koski *et al.*, 2015; Hicks *et al.*, 2016; Fantinato *et al.*, 2018a; Fantinato, 2019). Among temperate communities, species-rich grassland communities have been the subject of considerable attention. Indeed, they host a high diversity of animal-pollinated species (Fantinato *et al.*, 2016a, b; 2017; 2019b; Slaviero *et al.*, 2016), which can provide floral resources (i.e., nectar and pollen) to pollinators, thus effectively promoting their conservation (Fantinato *et al.*, 2019c). However, pollination interactions in species-poor communities have been largely overlooked and our understanding of their contribution to pollinator conservation is still lacking.

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Very recently pollination studies have shifted the focus from single plant communities to the landscape scale (Fantinato *et al.*, 2018b; Betts *et al.*, 2019; Hackett *et al.*, 2019). Landscape structure and composition influences the richness and abundance of pollinator populations, with diverse and complementary natural and semi-natural plant communities providing diverse and complementary sets of resources (Potts *et al.*, 2010). In complex landscapes, different plant communities with different structure and composition, and different vegetative and flowering phenology provide for higher and more stable availability of nectar and pollen resources, as well as overwintering refuges (Betts *et al.*, 2019). This is particularly true when different plant communities are deeply interconnected at the landscape scale through flows of energy and materials, naturally forming continuous patterns in response to environmental gradients (e.g., coastal plant communities, river and lake edges; Fantinato *et al.*, 2018b).

Marine-coastal ecosystems provide a particularly suitable example of plant communities spatially co-occurring at the landscape scale (Silan *et al.*, 2017; Del Vecchio *et al.*, 2018; 2019; Ivajnsič *et al.*, 2018). Among coastal ecosystems, saltmarshes are a major, widespread habitat in temperate zones and are characterized by high primary productivity and species diversity, representing habitat for migratory waterfowl, transient fish species and indigenous flora and fauna. Salt marshes typically occupy the upper intertidal zone, between land and open salt or brackish water (Allen & Pye, 1992; Adam, 2002). Within the Mediterranean region, they reach their greatest extent along the low-energy Northern Adriatic coastal area, which includes the Venice lagoon and the Po River Delta, characterized by the presence of lagoons, marshes and reclaimed lands. Although not particularly variable, the micro-topography, i.e. the small elevation gradients, induces a non-random, spatially correlated distribution of halophytic vegetation (Pignatti, 1966; Chapman, 1976) selecting plant species according to their tolerance to environmental factors like flooding periods, soil salinity and root oxygen availability. These factors ultimately determine a precise zonation of ecologically distinct halophytic communities (Chapman, 1976; Marani *et al.*, 2004; Ivajnsič *et al.*, 2018).

Saltmarshes occupy a critical interface between the land and the sea, where they provide important ecological and economic services, such as nutrient removal, storm protection, carbon sequestration, and habitats for numerous species of highly habitat specialized plants, fish, birds and invertebrates (Deegan *et al.*, 2012). Moreover, fringing many of the most anthropized soft coasts, saltmarshes often represent the dominant natural component in the mosaic of agricultural, urbanized and natural areas typical of marine-coastal landscapes (Del Vecchio *et al.*, 2016; Perillo *et al.*, 2019).

In light of these considerations, in the present study we assessed pollination interactions in saltmarshes considering all halophytic communities co-occurring at the landscape scale. Specifically, we addressed the issue by answering the following questions: (i) are there halophytic communities that contribute best to pollinator species richness in saltmarshes? (ii) Do plant species of different halophytic communities interact through pollinator sharing?

## Material and methods

### Study site

The study took place in the Venice lagoon which occupies an area of approximately 500 km<sup>2</sup> (mean depth 1.1 m, tidal range 0.6–1 m), with saltmarshes being mostly located in the SW and NE parts (Day *et al.*, 1998). Overall, saltmarshes occupy an area of nearly 4,000 ha, and are deeply interconnected with agricultural areas (mostly orchards; Buffa & Ghirelli, 2017). Specifically, data were collected in the Campalto saltmarshes (45°28'47"N; 12°18'07"E; Fig. 1), a well conserved example of saltmarshes (Francalanci *et al.*, 2013) extending for 16 ha in the northern portion of the Venice lagoon.

Halophytic communities of saltmarshes are generally characterized by a low richness of plant species showing a high habitat specialization, most of which are wind-pollinated graminoids (Ghirelli *et al.*, 2007). Given their importance for biodiversity conservation, halophytic communities are listed in Annex I of the EU Habitat Directive (92/43/EEC; Gigante *et al.*, 2018). According to Ivajnsič *et al.* (2018) at Campalto, proceeding from the lowest to the highest level along

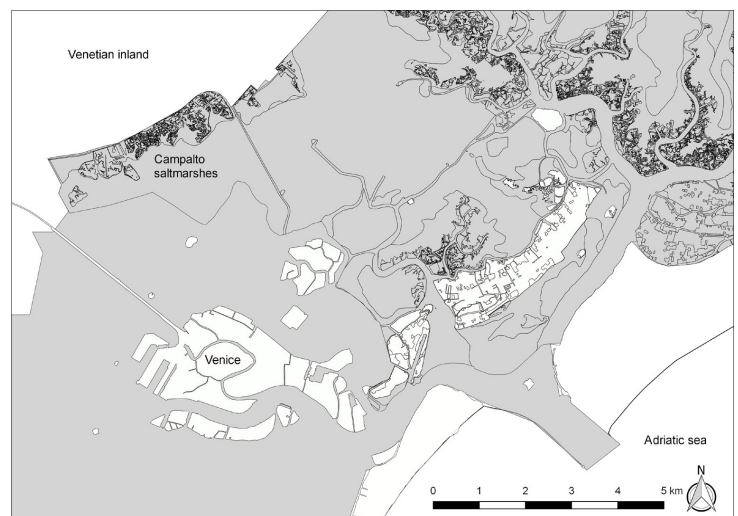


Fig. 1 - Map of the study site. Data were collected in the Campalto saltmarshes.

the marsh's elevation gradient, the typical transect of halophytic communities includes (i) the perennial saline rush marsh vegetation subjected to prolonged flooding regime, (ii) the vegetation of the sandbanks, mudflats and sandflats, (iii) the pioneer, irregularly flooded stands of annual succulent halophytes, (iv) the perennial saltmarsh vegetation dominated by succulent dwarf shrubs, and (v) the meso-eutrophic brackish swamp reeds (Tab. 1).

### Data collection

We identified halophytic communities and their spatial extent based on Ivajnsič *et al.* (2018). Based on a preliminary survey, animal-pollinated species only occurred in two halophytic communities: (i) the vegetation of sandbanks, mudflats and sandflats and (ii) the perennial saltmarsh vegetation dominated by succulent dwarf shrubs. All other halophytic communities hosted almost no animal-pollinated species.

At the beginning of the season we randomly placed 20 permanent plots (1 m × 1 m) in each of the two halophytic communities, for a total of 40 plots. In each plot, the presence of animal-pollinated species was recorded, and their flowering phenology was monitored every fifteen days, from the beginning (01-08-2017) to the end of the flowering season (01-10-2017), for a total of five surveys. Flowering monitoring started at the opening of the first flower and ended when individual plants no longer possessed any flower with anthers (Fantinato *et al.* 2016a). Moreover, once a month (12-08-2017; 11-09-2017; 15-10-2017) we recorded the total coverage of visual displays per species and the visiting pollinators by counting the number of visits to each plant species. Depending on the species, a visual display consisted of a single flower, an inflorescence or a group of flowers occurring together in a recognisable visual unit (Hegland & Totland, 2005). Each plot

was monitored for 10 minutes (from 10 a.m. to 4 p.m.) in warm and sunny days, for a total of 1,200 minutes. Both plants and pollinators were identified at the level of species or morphospecies.

### Data analysis

To estimate the overall species richness of pollinators in the targeted halophytic communities, we built plot-based rarefaction curves (Gotelli & Colwell, 2001). Specifically, we pooled data recorded in each plot during the three surveys. We computed the accumulation curves using the cumulative number of plots sampled per halophytic community. Moreover, since we sampled halophytic communities subjected to different environmental conditions, which might possibly lead to differences in pollinator activity, for each halophytic community we evaluated the sampling completeness of pollinator species by using the Chao 2 estimator of asymptotic species richness (Colwell *et al.*, 2004). We chose Chao 2 estimator because it is one of the least biased estimates for a small number of samples (Chao *et al.*, 2009; Chacoff *et al.*, 2012). Pollinator species richness was calculated by quantifying the percentage of the asymptotic richness detected by the observed one. The accumulation curves and the Chao 2 estimator were calculated with the R-based package Vegan (Oksanen *et al.*, 2013).

To test whether plant species of different halophytic communities interact through pollinator sharing we compared each plant species spectrum of pollinators through one-way PERMANOVA applying the Bray-Curtis similarity index with 9,999 randomizations (Anderson & Ter Braak, 2003), using contacts recorded in each plot as replicates. No significant differences would reveal pollinator sharing between plant species. All calculations were done within the R statistical framework (R Development Core Team 2012).

Tab. 1 - List of plant communities occurring in the Campalto saltmarshes. For each plant community we reported the correspondent phytosociological association, the list of dominant plant species, the mean elevation ( $\pm$  SD) on the average sea level according to Ivajnsič *et al.* (2018), and the correspondent Nature 2000 habitat.

Plant community	Phytosociological association	Dominant species	Mean elevation (m) $\pm$ SD (m)	Natura 2000 habitat
Perennial saline rush marsh vegetation subjected to prolonged flooding regime	<i>Puccinellio festuciformis - Juncetum maritimi</i> (Pignatti 1953) Géhu et Scoppola in Géhu <i>et al.</i> 1984	<i>Juncus maritimus</i> Lam., <i>Puccinellia festuciformis</i> (Host) Parl.	0.26 $\pm$ 0.09	1410
Vegetation of sandbanks, mudflats and sandflats	<i>Limonio narbonensis - Puccinellietum palustris</i> (Pignatti 1966) Géhu et Scoppola in Géhu <i>et al.</i> 1984	<i>Limonium narbonense</i> Mill., <i>Sporobolus maritimus</i> (Curtis) P.M. Peterson & Saarela	0.30 $\pm$ 0.05	1320
Pioneer, irregularly flooded stands of annual succulent halophytes	<i>Salicornietum venetae</i> Pignatti 1966	<i>Salicornia veneta</i> Pignatti & Lausi	0.31 $\pm$ 0.07	1310
Perennial salt-marsh vegetation dominated by succulent dwarf shrubs	<i>Puccinellio festuciformis - Artrocnetum fruticosae</i> (Br.-Bl. 1928) Géhu 1976	<i>Salicornia fruticosa</i> (L.) L., <i>Puccinellia festuciformis</i> (Host) Parl.	0.37 $\pm$ 0.08	1420
Meso-eutrophic brackish swamp reeds	Aggr. <i>Thinopyrum acutum</i> (DC.) Banfi; Aggr. <i>Phragmites australis</i> (Cav.) Trin. ex Steud.	<i>Thinopyrum acutum</i> (DC.) Banfi, <i>Phragmites australis</i> (Cav.) Trin. ex Steud.	0.49 $\pm$ 0.08	-

## Results

In the study site we identified three animal-pollinated species. Specifically, we recorded two animal-pollinated species in the vegetation of sandbanks, mudflats and sandflats, while one in the perennial saltmarsh vegetation dominated by succulent dwarf shrubs (Tab. 2). *Limonium narbonense* and *Limbarda chritmoides* flowered for almost 5 decades and showed synchronous flowering periods (from 01-08-2017 to 15-09-2017). On the other hand, *Galatella pannonica* flowered for almost eight decades and its flowering period overlapped with those of *Limonium narbonense* and *Limbarda chritmoides* for only 3 decades (from 15-08-2017 to 31-10-2017). However, though only three animal-pollinated species could be observed in saltmarshes, the coverage of their visual displays during the peak of flowering was relatively high, with inflorescences of *Limonium narbonense* covering  $50.00\% \pm 26.00\%$  (mean  $\pm$  SD), those of *Limbarda chritmoides*  $4.45\% \pm 3.53\%$  and those of *G. pannonica*  $10.55\% \pm 8.53\%$  of the plot surface.

Overall, we recorded 222 pollination contacts between the three plant species and nine pollinator species (Tab. 2). Pollinator species belonged to three orders, i.e., *Diptera* (five species), *Hymenoptera* (two species), and *Lepidoptera* (two species). The most visited plant species was *Limonium narbonense* (146 contacts with six pollinator species), followed by *G. pannonica* (45 contacts with seven pollinator species) and *Limbarda chritmoides* (31 contacts with three pollinator species). Sampling completeness revealed that we detected the 100% of pollinator species in both the vegetation of sandbanks, mudflats and sandflats, and the perennial saltmarsh vegetation dominated by succulent dwarf shrubs. Overall, the richness of pollinator species was higher in the vegetation of sandbanks, mudflats and sandflats (9 pollinator species), than in the perennial saltmarsh vegetation dominated by succulent dwarf shrubs (3 pollinator species; Fig. 2).

Animal-pollinated species of saltmarshes only partially shared pollinator species, with significant differences revealed by the PERMANOVA ( $F = 8.118$ ;  $P = 0.001$ ; d.f. = 1). In other words, the two different halophytic communities are not interconnected through pollination interactions. *Apis mellifera* L. (1758) was so far the most frequent pollinator of *Limonium narbonense* (Tab. 2; Fig. 3); while *Simuliidae* sp. 1 of *Limbarda chritmoides* (Tab. 2; Fig. 3). On the other hand, *G. pannonica* got into contact with a wider variety of pollinators than the first two plant species, and no markedly dominant pollinator species could be observed (Tab. 2; Fig. 3).

## Discussion

Overall, in the saltmarshes of the Venice lagoon we observed only three species depending on animals for their pollination. Despite the relative low number of plant species pollinated by animals, animal-mediated pollination should not be considered secondary among biotic interactions in saltmarshes. Indeed, *Limonium narbonense*, *Limbarda chritmoides* and *Galatella pannonica* are especially widespread in the Venice lagoon (Marani *et al.*, 2006; Rizzetto and Tosi, 2012), possibly contributing to local pollinator conservation.

There is general agreement that the richness of plant species positively influences the richness of pollinator species (Holzschuh *et al.*, 2007; Sároszpatáki *et al.*, 2009), which has been explained by the increase of floral resource heterogeneity (nectar and pollen) and quantity, which increases the attractiveness for many pollinator species seeking single and multiple resources (Ghazoul, 2006). This, in turn, has led pollinator conservation programs to focus mostly on species rich plant communities. However, Fantinato *et al.* (2018a) showed that in coastal dune ecosystems, richness of animal-pollinated plants and pollinators may not be necessarily correlated, with few plant species sustaining the majority of pollinator species.

Tab. 2 - List of animal-pollinated species recorded in the Campalto saltmarshes. For each animal-pollinated species we reported its plant community, the flowering period, the inflorescence coverage in the plots (mean  $\pm$  SD) during the peak of flowering, and the list of visiting pollinators.

Animal-pollinated species	Plant community	Flowering period	Inflorescence coverage (%; mean $\pm$ SD) at the peak of flowering	Visiting pollinators	Total number of contacts
<i>Limonium narbonense</i> Mill.	Vegetation of sandbanks, mudflats and sandflats	from 01-08-2017 to 15-09-2017	$50.00\% \pm 26.00\%$	<i>Apis mellifera</i> (L., 1758), <i>Bombus terrestris</i> (L., 1758), <i>Odontomyia angulata</i> (Panzer, 1798), <i>Sphaerophoria scripta</i> (L., 1758), <i>Pontia edusa</i> (Fabricius, 1777), <i>Vanessa cardui</i> (L., 1758)	146
<i>Limbarda chritmoides</i> (L.) Dumort	Perennial salt-marsh vegetation dominated by succulent dwarf shrubs	from 01-08-2017 to 15-09-2017	$4.45\% \pm 3.53\%$	<i>Apis mellifera</i> (L., 1758), <i>Sphaerophoria scripta</i> (L., 1758), <i>Simuliidae</i> sp. 1	31
<i>Galatella pannonica</i> (Jacq.) Galasso, Bartolucci & Ardenghi	Vegetation of sandbanks, mudflats and sandflats	from 15-08-2017 to 31-10-2017	$10.55\% \pm 8.53\%$	<i>Apis mellifera</i> (L., 1758), <i>Eristalinus aeneus</i> (Scopoli, 1763), <i>Eristalis pertinax</i> (Scopoli, 1763), <i>Sphaerophoria scripta</i> (L., 1758), <i>Simuliidae</i> sp. 1, <i>Pontia edusa</i> (Fabricius, 1777), <i>Vanessa cardui</i> (L., 1758)	45

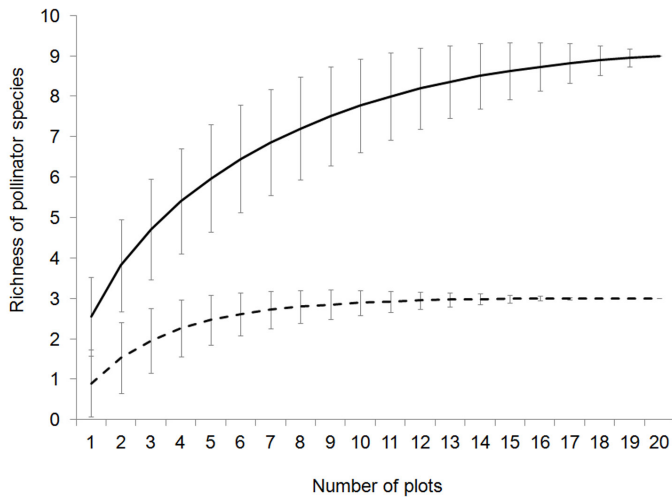


Fig. 2 - Accumulation curves of the richness of pollinators. Accumulation curves were computed by using the cumulative number of plots sampled per plant community as the unit of sampling effort. Plant communities were represented by different colours; black continuous line: the vegetation of sandbanks, mudflats and sandflats, grey dashed line: the perennial saltmarsh vegetation dominated by succulent dwarf shrubs.

Our results revealed that, such as in coastal dunes, also in saltmarshes a few animal-pollinated species are responsible for the maintenance of the pollinator community. Indeed, though we recorded only three animal-pollinated species, we showed that mass flowering can provide abundant resources to pollinators, possibly contributing to their conservation. Species of genus *Limonium* have been proved to be important sources of nectar for many pollinator species (Sei & Porter, 2006; Zhang *et al.*, 2015). Similarly, species belonging to the family of *Asteraceae*, e.g. *Limbaria chritmoides* and *G. pannonica*, are pollen and nectar rewarding, and they generally receive many kinds of pollinators (Willmer, 2011). Moreover, the relatively late flowering season of the three species, which is markedly centred at late summer – early autumn, guarantees floral resources for pollinators also during a period of the year in which flowering events are almost completed in the majority of plant communities (e.g., Fantinato *et al.*, 2016a, 2018b).

When comparing halophytic communities in terms of richness of pollinator species, the vegetation of sandbanks, mudflats and sandflats emerged as the richest one. The presence of two attractive animal-pollinated species with poorly overlapping flowering periods (i.e., *Limonium narbonense* and *G. pannonica*) makes floral resources to pollinators available for a longer flowering season than in the perennial saltmarsh vegetation dominated by succulent dwarf shrubs. However, it is worth to consider that *Limbaria chritmoides*, while being poorly visited, showed an almost comple-

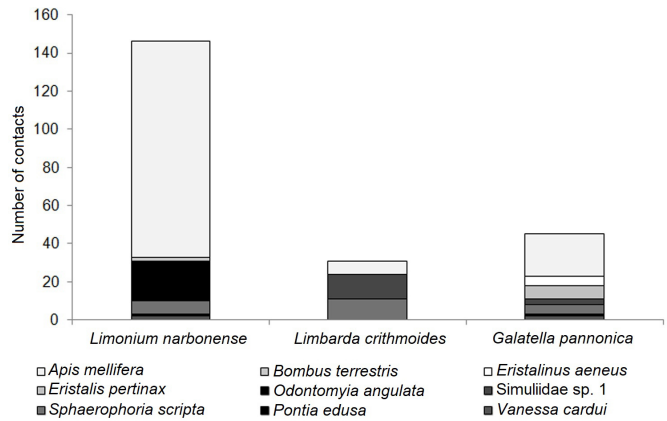


Fig. 3 - Abundance of pollinator species for the three animal-pollinated species recorded in saltmarshes.

mentary spectrum of pollinators with the co-flowering species *Limonium narbonense*, thus playing an important role for the maintenance of at least a portion of the pollinator community of saltmarshes.

From an ecological point of view, co-flowering species are likely to experience strong competition for pollinators and potentially suffer high pollen loss and fitness decrease (Fang & Huang, 2013; Van der Kooi *et al.*, 2016). Adaptations to minimize competition and pollen loss may include specialization on different pollinators or disjointed flowering periods (Muchhala *et al.*, 2010; Kipling & Warren, 2014; Ruchisansakun *et al.*, 2016), which can ultimately allow animal-pollinated species to spatially co-occur (Fantinato *et al.*, 2018a).

## Conclusion

Our study proved that, when different plant communities are spatially co-occurring, the assessment of pollination interactions at the landscape scale results in a better understanding of their contribution to pollinator conservation. While being overlooked in pollination studies, the overall late flowering season and the high local abundance of animal-pollinated species in the halophytic communities of saltmarshes, make them an important component of the landscape for the pollinator conservation purpose. Being characteristic of a diversified landscape, in which natural and agricultural areas coexist, halophytic communities of saltmarshes can crucially contribute to the pollination service retention by providing a foraging habitat for pollinators. Further development of the present study should improve the comprehension of pollination interactions by including the more inland plant communities. This would reveal possible pollinator exchanges between the plain and the lagoon, ultimately providing important information for the definition of a systemic plan for the conservation of pollinators.



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