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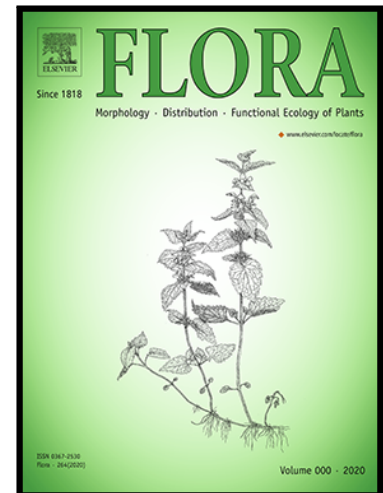
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## **Pollinator distribution in patches of suitable habitat depends more on patch isolation than on floral abundance**

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### **Highlights**

- Pollinator distribution in patches of suitable habitat depends on patch isolation
- Floral abundance alone does not assure pollinator occurrence
- Landscape matrix permeability depends on pollinator movement ability and behaviour
- Pollination interactions at landscape scale have a clear spatial component
- Spatial patterns of plant reproductive success depend on pollinator distribution

### **Abstract**

Intrinsic complexity of real-world systems makes particularly difficult to decipher which factors influence the dispersal of pollinators in the landscape matrix and their distribution among patches of suitable habitat. Saltmarshes are an ideal and naturally simplified landscape to study the ability of different groups of pollinators to disperse across a landscape matrix, as they consist of a matrix of flooded areas surrounding patches of suitable habitat with different degrees of isolation from the mainland and different levels of floral abundance. We hypothesise that pollinator distribution to flowering plants depends more on patch isolation than on floral abundance with pollinator richness and visitation rates to flowering plants decreasing with increasing distance from the mainland. To this end, we established 60 permanent plots at varying distances from the mainland and monitored pollinator visitation to entomophilous plants. We also quantified the reproductive success of

entomophilous species in the surveyed plots by calculating fruit set. We found that the pollinator community of saltmarshes consisted only of flying pollinators with good dispersal abilities, while we recorded no flightless pollinator species. Both pollinator richness and visitation rate decreased with increasing distance of patches of suitable habitat from the mainland, affecting reproductive success of a non-autogamous entomophilous species. Interestingly, floral abundance did not affect pollinator richness and visitation rate to flowering plants, nor did it affect reproductive success of target plant species. In saltmarshes, the pollinator distribution depends more on patch distance from the mainland than on floral abundance. Our results suggest that the presence of patches of suitable habitat in a landscape matrix does not necessarily ensure the maintenance of pollinators. Rather, our results suggest that suitable habitat isolation is the critical factor in pollinator dispersal and distribution that should be considered to improve landscape matrix permeability to pollinators.

### **Keywords**

Island biogeography; Landscape matrix; Plant reproduction; Pollination; Pollinator distribution; Saltmarshes.

### **Author Contributions**

**Edy Fantinato:** Conceptualization, Methodology, Formal analysis, Supervision, Writing - Original Draft, Writing - Review & Editing **Sebastiano Favarin:** Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing **Gabriella Buffa:** Writing - Original Draft, Writing - Review & Editing

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## 1. Introduction

Intrinsic complexity of real-world systems makes particularly difficult to decipher which factors influence species dispersal in the landscape matrix and their distribution among patches of suitable habitat (Häkkinen et al., 2017; Newman et al., 2019). The issue is particularly relevant when considering organisms that are functionally important for maintaining biodiversity over time (Diniz et al., 2021), such as apex predators, seed dispersers and pollinators (Harvey et al., 2017). Because most flowering plants rely on animals for pollination, changes in the spatial distribution of pollinators can have serious consequences for plant sexual reproduction and the maintenance of plant diversity (Thomson et al., 2019). The strict interconnection between pollinator distribution and plant conservation is particularly evident given the ongoing global pollinator decline (Nicolson and Wright, 2017), with plant population conservation threatened by local extinctions of pollinator species (Kaiser-Bunbury et al., 2010).

Theoretical models and empirical evidence suggest that pollinator distribution is the result of a range of factors operating at different spatial and temporal scales (Pellissier et al., 2018). These factors have been summarised in the Assembly Rules conceptual framework (Götzenberger et al., 2012). The interplay between historical patterns of speciation, large-scale migration processes and environmental filtering determines the large-scale range of pollinator species (Tojo et al., 2017). Within range boundaries, landscape composition and configuration influence pollinator dispersal in relation to their ability to move (Bommarco et al., 2010). Dispersal success of pollinators between spatially separated patches of suitable habitat is strongly related to their isolation. However, the degree of isolation depends not only on the spatial distance between habitat patches, but also on the nature of the landscape matrix (Jauker et al., 2009; Poniowski et al., 2016). For example, the dispersal of different pollinator taxa has been shown to change in agricultural and urbanised

landscapes, with the intensity of landscape modification playing a key role in determining pollinator presence and distribution (e.g., [Carvalho et al., 2010](#); [Verboven et al., 2014](#)).

The dispersal of pollinators between patches of suitable habitat is often associated with the theory of island biogeography of [MacArthur and Wilson \(1967\)](#), which compares patches of suitable habitat, e.g., patches where pollinators can find nesting sites and/or floral resources, to oceanic islands surrounded by a hostile matrix of unsuitable habitat ([Haila, 2002](#); [Laurance, 2008](#)). However, pollinator species move between patches of suitable habitat in response to varying degrees of landscape matrix permeability. Studies report contrasting results when considering pollinators with different dispersal abilities and when floral diversity and abundance vary (e.g., [Jauker et al., 2009](#); [Öckinger et al., 2018](#)). Indeed, the distribution of pollinators is thought to be determined by spatial patterns of floral diversity and abundance ([Biella et al., 2019](#), [Fantinato et al., 2021](#)), leading to interspecific competitive and/or facilitative interactions among plants for pollinators ([Fantinato et al., 2018](#); [Bergamo et al., 2019](#)), as well as interspecific exploitative competition for shared floral resources among pollinator species ([Thomson and Page, 2020](#)). Recently, however, [Reverté et al. \(2019\)](#) showed that spatial variation in floral abundance is a poor predictor of pollinator distribution, highlighting the difficulty in deciphering the contribution of different factors in influencing pollinator dispersal and distribution ([Newman et al., 2019](#)).

Saltmarshes represent an ideal ecosystem to study the ability of different groups of pollinators to disperse across a landscape matrix, as they are part of transitional areas that are flooded daily by cyclical tides ([Ivajnsič et al., 2018](#)). This may prevent flightless pollinators and ground-nesting pollinators from reaching long distances from land areas that are permanently above sea level (i.e., the mainland). From the island biogeography perspective ([MacArthur and Wilson, 1967](#)), saltmarshes can be viewed as a landscape matrix composed of only one land cover type, where patches of floral resources, varying in distance from the mainland, can be considered as patches of suitable habitat to which pollinators migrate to gather floral resources. In addition, among plant species of saltmarshes, only a small number is pollinated by animals, but these plants can reach high local abundance and occur over wide areas ([Davidson et al., 2020](#)). To ensure pollination under the stressful environmental conditions of saltmarshes, entomophilous plants exhibit a number of adaptations, including autogamy and disjunct mass flowering periods to minimise interspecific competition for pollinators ([Fantinato and Buffa, 2019](#)). The temporal sequence of mass flowering of monospecific stands makes saltmarshes a

naturally simplified landscape consisting of a matrix of flooded areas surrounding patches of suitable habitat with individual flowering species of varying floral abundance.

In this study, we used saltmarshes as a model landscape to investigate issues related to pollinator dispersal and distribution. Accordingly, we asked the following questions: How do pollinator richness and visitation rates change in patches of suitable habitat with different degrees of isolation (i.e., distance from the mainland) and different levels of floral abundance? How can pollinator movement abilities (i.e., flightless vs. flying) and feeding and reproductive behaviour be used to interpret differences in pollinator dispersal in a landscape matrix? How does the dispersal of pollinators in a landscape matrix affect the reproductive success of flowering plants with different pollination strategies (i.e., non-autogamous vs. facultatively autogamous species)? We hypothesise that pollinator richness and visitation rates to flowering plants decrease with increasing distance from the mainland (1<sup>st</sup> hypothesis), and that the distribution of pollinators to flowering plants depends on their movement abilities (i.e., flightless vs. flying) and feeding and reproductive behaviour (2<sup>nd</sup> hypothesis). In addition, we hypothesise that the reproductive success of non-autogamous plants is particularly influenced by variation in pollinator distribution, with reproductive success increasing with increasing proximity to the mainland (3<sup>rd</sup> hypothesis).

## **2. Materials and methods**

### **2.1 Study site**

The study took place in the saltmarshes of Campalto (45°28'47"N; 12°18'07"E; Fig. 1), a well-preserved saltmarsh of almost 16 ha in the north-western part of the Venice Lagoon, Italy (Francalanci et al., 2013). The study focused on a well delimited portion of the Venice Lagoon to fix the influence of the landscape matrix on the pollinator community. Saltmarshes of the Venice Lagoon are located just above mean sea level, from 0.0 m to about 0.7 m (Rizzetto and Tosi, 2012) and are inundated twice a day by tides (Marani et al., 2004). The tidal regime is microtidal with a range of 0.6 m – 1.0 m (Cucco et al., 2009). Saltmarshes of the Venice Lagoon are characterised by a complex landscape that includes intertidal channels, and relatively flat areas. Although the microtopography shows low variability, it causes a non-random, spatially correlated distribution of halophytic vegetation (zonation) (Chapman, 1976; Marani et al., 2004) by influencing other environmental parameters,

e.g., flooding times, oxygen availability for roots, soil salinity (Ivajnsič et al., 2018). The succession of halophytic communities includes (from lowest to highest marsh elevation) (i) perennial saline rush vegetation exposed to prolonged inundation, (ii) daily inundated vegetation of sandbanks, mudflats and sandflats, (iii) pioneer irregularly flooded stands of annual succulent halophytes, (iv) perennial saltmarsh vegetation dominated by succulent dwarf shrubs, and (v) mesoeutrophic brackish marsh reed (Ivajnsič et al., 2018). In the present study, data were collected on the vegetation of sandbanks, mudflats and sandflats, which host the most abundant populations of entomophilous plants of Venice Lagoon saltmarshes, namely *Limonium narbonense* Mill. and *Galatella pannonica* (Jacq.) Galasso, Bartolucci & Ardenghi (i.e., *Aster tripolium* L.; Fantinato and Buffa, 2019).

*Limonium narbonense* is an herbaceous perennial hemicryptophyte, belonging to the family of Plumbaginaceae, with leaves arranged in a basal rosette and 30 – 70 cm tall, hairless, robust, and with cylindrical stems densely branched at the top. Its inflorescence is a highly branched corymbose panicle with funnel-shaped violet-blue flowers 5.5 – 6.5 mm in diameter. The flowering period of *L. narbonense* ranges from June to September, with peak flowering in late August – early September (Fantinato and Buffa, 2019). *G. pannonica* is an herbaceous biennial hemicryptophyte, belonging to the family of Asteraceae, with a short epigeogenous rhizome, an erect stem with a basal rosette consisting of oblanceolate-spatulate leaves with petioles. The stem is swollen at the base, striated and branched at the top with a maximum height of 120 cm. The inflorescence is a corymbothyrsum with several capitula of 2 – 3 cm in diameter with pink or blue ray florets and yellow tubular disc florets. The flowering period of *G. pannonica* ranges from August to October, with a peak flowering period in late September – early October (Fantinato and Buffa, 2019). Although studies on the self-compatibility of the target species for the study site are lacking, studies conducted at different sites in the species' range indicate that *L. narbonense* exhibits heteromorphic sporophytic self-incompatibility (Baker, 1966; Cortinhas et al., 2015), whereas *G. pannonica* is a facultatively autogamous species (Koutstaal et al., 1987; Kühn et al., 2004).

## 2.2 Data collection

Prior to the onset of flowering, we established ten permanent belt transects using a GPS device. A belt transect consists of contiguous or spaced sampling plots laid out along the direction of an environmental gradient (Del Vecchio et al., 2019; Kent and Coker, 1992), which in the present study is the gradient between land areas that

are permanently above sea level (hereafter, the mainland), and specifically the lagoon bank, and the water body. The distance between transects was set at 50 m. Along each transect and in correspondence with the vegetation of sandbanks, mudflats and sandflats, we selected six 1 m × 1 m plots at least 50 m apart from each other. The distance of the plots from the mainland ranged from 0.8 m to 570.7 m. Overall, we monitored 60 plots (six plots × ten transects). Plant communities and their spatial extent were retrieved from Ivajnsič et al. (2018). For each plot, we measured the distance from the mainland using the ‘Convert Lines to Points’ and ‘Distance to nearest hub’ SAGA tools (GRASS version 7.8.2; plugin for QGIS version 3.10).

Since inflorescences of target species were particularly dense, we quantified floral abundance by visually estimating the percent cover of inflorescences in each plot during peak flowering of *L. narbonense* (from 31/08/2020 to 09/09/2020) and during peak flowering of *G. pannonica* (from 23/09/2020 to 30/09/2020). The percent cover of inflorescences was estimated as vertical projection of inflorescences on the ground as viewed from above. Both target species occurred in all sampled plots. Because the target species have disjunct mass flowering times, only one species was observed flowering during each survey. We also recorded pollination interactions between flowering species and flower visitors during each survey. Therefore, each plot was monitored for 14 minutes each time, divided into two 7- min subsets (one between 10 a.m. and 1 p.m., and one between 1 p.m. and 4 p.m.) to ensure observation of pollinators with different daily activity times on sunny and windless days (Fantinato et al., 2019). We considered visitors as pollinators if they made direct contact with the reproductive organs of the flower and visited the flower for > 1 s (Hegland and Totland, 2005). Overall, we monitored plant-pollinator interactions for 1,680 min and identified pollinators ( $S = 52$ ) to species or morphospecies. Only 12 species, including all butterfly species, *Apis mellifera*, *Bombus pascuorum*, *Episyrrhus balteatus* and *Eristalis tenax* were identified by sight, all other flower visitors were collected and identified in the laboratory using Ball and Morris (2013), Falk and Lewington (2015), Chinery (2012) and Villa et al. (2009). All samples are stored in the entomological collection of Ca' Foscari University. In the first survey, we marked 3 panicles of *L. narbonense* belonging to different individuals per plot, while in the second survey we marked 6 capitula belonging to different individuals of *G. pannonica* per plot. At the end of the flowering period of each species, we carefully collected the marked inflorescences and stored them in paper bags. We counted the total number of flowers on each panicle and capitulum and then randomly selected 20 flowers to determine the



number of fertilised flowers. Using a stereomicroscope, we dissected and counted the number of enlarged (fertilised) or shrunken ovules (without the presence of embryos) to determine fruit set (Snow, 1982).

### 2.3 Data analysis

We used the percent cover of inflorescences and the distance from the mainland to explain the distribution of pollinators on the flowering plants of the vegetation of the sandbanks, mudflats and sandflats. Our first hypothesis was that not only is the presence and abundance of flowering plants a prerequisite for the occurrence of pollinators, but also that the distance from the mainland may have an effect on the richness and visitation rate of pollinators. Moreover, we hypothesise that distribution of pollinators to flowering plants depends on their movement ability (i.e., flightless vs. flying) and feeding and reproductive behaviour (2<sup>nd</sup> hypothesis).

To explain pollinator distribution on target plants, we built two different Generalised Linear Models (GLMs) for *L. narbonense* and *G. pannonica*. In the first model we included pollinator species richness as the dependent variable and percent inflorescence cover, distance from the mainland, and their interaction (namely, inflorescence cover  $\times$  distance from the mainland) as independent variables, while in the second model, we used pollinator visitation rate (i.e., the number of pollinators observed for 14 minutes, i.e., the duration of one survey) as dependent variable. We also included the quadratic term of percent inflorescence cover and distance from the mainland as independent variables in the GLMs to account for possible non-linear relationships. To test whether different orders of pollinators showed different responses to the independent variables, we performed further GLMs by looking separately at the richness and visitation rate of Hymenoptera (including bees and wasps) and Diptera to *L. narbonense* and *G. pannonica*. We chose to consider only Hymenoptera and Diptera because they were the richest and most abundant among all pollinator orders recorded. Likelihood ratio tests (LRT; drop1 function; package stats) were used to test the significance of the models, which were simplified by backward elimination of non-significant independent variables. Poisson distributions (and log as link function) were appropriate for most models, with the exception of the models for total visitation rate and visitation rate of Hymenoptera to *G. pannonica*, which were over-dispersed (dispersiontest function; package AER; Kleiber and Zeileis, 2008), and for which negative binomial distributions were used (O'Hara and Kotze, 2010).

Finally, our third hypothesis was that reproductive success of non-autogamous plants is particularly influenced by variation in pollinator distribution, with reproductive success increasing with increasing proximity to the

mainland. To test whether patterns of pollinator distribution influenced the reproductive success of entomophilous plants, we assessed the reproductive success of each target plant species by calculating the fruit set of each marked inflorescence. To test whether reproductive success of *L. narbonense* and *G. pannonica* was related to percent inflorescence cover and distance from the mainland, we performed Generalized Linear Mixed Models (GLMMs; glmr function; package lme4; Bates et al., 2015) with Gamma error distribution and log as link function, using fruit set per panicle or capitulum as the dependent variable, percent inflorescence cover, distance from the mainland, and their interaction as independent variables, and plot identity as random factor. Models were simplified by backward elimination of non-significant independent variables. All analyses were performed using R version 4.1.3 (R Core Team, 2018).

### 3. Results

We recorded a total of 1584 visits by 52 pollinator species to *Limonium narbonense* and *Galatella pannonica*. Of the 52 pollinator species, 22 were Hymenoptera, 18 Diptera, 8 Lepidoptera and 4 Hemiptera. No flightless pollinator species were recorded. The richness of pollinator species interacting with *L. narbonense* was 33 (for a total of 643 visits; Table 1), and that of *G. pannonica* was 36 (for a total of 935 visits; Table 1). Inflorescence cover of the two entomophilous plants was relatively uniform, with *L. narbonense* inflorescence cover ranging from 35% to 65%, with an average cover of  $48.66\% \pm 8.82\%$  (mean  $\pm$  SD), and that of *G. pannonica* ranging from 40% to 60%, with an average cover of  $46.92\% \pm 6.83\%$  of the plot area.

Consistent with our first hypothesis, we found that both pollinator richness and visitation rate were affected to some extent by distance from the mainland. Specifically, the richness of pollinator species visiting *L. narbonense* showed a significant negative relationship with distance from the mainland (Table 2; Fig. 2), whereas no significant relationship was found for the richness of pollinator species visiting *G. pannonica* (Table 2). Regardless of plant identity, the rate of pollinator visitation (i.e., the number of pollinators observed during a survey in a plot) decreased significantly with increasing distance from the mainland (Table 2; Fig. 2; Fig. 3). When considering the richness of pollinators belonging to different orders separately, we found a significant negative relationship only between the richness of Hymenoptera visiting *L. narbonense* and the distance from the mainland (Table 2; Fig. 2), while no significant relationship emerged when considering Hymenoptera

visiting *G. pannonica* and Diptera visiting either plant species (Table 2). As for the visitation rate of pollinators, we found a significant negative relationship between the visitation rate of Hymenoptera and the distance from the mainland, in both plant species (Table 2; Fig. 2; Fig. 3). On the other hand, only for *L. narbonense* we found a significant relationship between the visitation rate of Diptera and the distance from the mainland. In particular, the visitation rate of Diptera showed a significant hump-shaped relationship with distance from the mainland (Table 2; Fig. 2), suggesting that the visitation rate of Diptera to *L. narbonense* reaches maximum values at intermediate distances.

In agreement with our third hypothesis, the fruit set of *L. narbonense* decreased significantly with increasing distance from the mainland (Table 3; Fig. 4); in other words, the reproductive success of *L. narbonense* increased with increasing proximity to the mainland. No significant relationship was found between the fruit set of *G. pannonica* and distance from the mainland (Table 3).

Percent inflorescence cover did not affect pollinator species richness and visitation rate to flowering plants, nor did it affect reproductive success of target plant species.

#### 4. Discussion

In agreement with our first hypothesis, our results suggest that the distribution of pollinators in saltmarshes is influenced by the distance of patches of suitable habitat from the mainland. Moreover, consistent with our second hypothesis, our observations revealed that the pollinator community of saltmarshes consists only of flying pollinators with good dispersal abilities, while we recorded no flightless pollinator species (e.g., ants, juveniles of bush crickets). Flightless pollinators are common in pollination networks of transitional and coastal ecosystems such as coastal scrubs and mixed pine forest (Herrera, 1984) and dunes (Fantinato, 2019). This suggests that the effect of daily flooding may prevent migration of flightless pollinators into patches of suitable habitat in saltmarshes. However, the pollinators recorded (which have good flight capabilities) also showed a clear spatial pattern of occurrence, with the richness of pollinator species visiting *Limonium narbonense* and the visitation rate to both *L. narbonense* and *Galatella pannonica* being negatively related to the distance from the mainland.

Our results can be interpreted in terms of the theory of island biogeography (MacArthur and Wilson, 1967), which indeed predicts that islands closer to the mainland are more likely to be colonized than distant islands. However, differences emerged when considering the spatial distribution of Hymenoptera and Diptera. While the species richness and visitation rate of Hymenoptera showed a negative relationship with the distance from the mainland for *L. narbonense*, the species richness of Diptera did not show significant relationships and the visitation rate followed a hump-shaped relationship. The same pattern was found for the visitation rate of Hymenoptera to *G. pannonica*, while no significant relationship was found when considering either the species richness of Hymenoptera or the richness and visitation rate of Diptera. In fact, the two groups exhibit differences in their life cycles and feeding and reproductive behaviours that may determine their aptitude to move across the landscape and ultimately their pollination ability (Mizunaga and Kudo, 2017; Borkent and Schlinger, 2008). The main differences in reproductive behaviour between most Hymenoptera and Diptera is due to their ability to build and use a nest for their larvae. Indeed, most Hymenoptera in Mediterranean and temperate regions are considered ‘central foragers’ (Pyke, 1984). Central foragers generally centre their foraging area in correspondence with the nest site, with the size of the foraging area depending on the flight ability of the pollinator (Ricketts et al., 2008). Migrations between the nest and the foraging area may require high energy demands due to the continuous provisioning of the nest, since Hymenoptera must seek resources for themselves as well as their larvae (Kearns, 1992). Since saltmarshes are flooded daily, they do not provide a suitable nesting substrate for ground-nesting Hymenoptera. Moreover, since saltmarshes are dominated by herbaceous plant species, Hymenoptera nesting in woody structures would not find suitable support either (Potts et al., 2005). For this reason, ground- and wood-nesting Hymenoptera might move to saltmarshes only to forage, and therefore develop most pollination interactions with plants growing near the mainland, namely near their nesting sites, to avoid wasting energy in their foraging migrations (Pyke, 1984).

The only significant relationship we found when considering Diptera was a hump-shaped relationship between the visitation rate to *L. narbonense* and the distance from the mainland. In other words, *L. narbonense* was more frequently visited by Diptera when it grew at an intermediate distance from the mainland. One possible explanation is that the large number of Hymenoptera near to the mainland could lead to competitive interactions for floral resources with Diptera, which would then be forced to move towards the water body (Sargent and Ackerly, 2008). Competitive behaviour has often been observed between pollinators, particularly between

Hymenoptera and Diptera, with Hymenoptera being considered stronger competitors compared to Diptera (Cadotte and Tucker, 2017). Since Diptera do not build nests or provide parental care, they do not have to make constant foraging migrations and have much lower energy requirements than Hymenoptera (Pyke, 1984). Furthermore, Diptera may use flowers not only for foraging, but also as a source of warmth, shelter, and mating opportunities (Woodcock et al., 2014), suggesting that daily inundation does not affect their dispersal and distribution in saltmarshes as it does for Hymenoptera. In this context, the fact that no significant relationship was found between the visitation rate of Diptera to *G. pannonica* and the distance from the mainland could be due to the differences in the floral morphology of the two plant species. The relatively small, funnel-shaped flowers of *L. narbonense*, which form branched, corymbose panicles, might prevent different pollinators from searching for floral resources simultaneously on the same flower (Pellissier et al., 2010). In addition, pollinators are forced to visit multiple flowers in succession to collect floral resources, limiting their residence time and potentially disturbing less competitive pollinators. In contrast, the capitula of *G. pannonica* that form corymbothsyrus inflorescences could be considered a less restrictive floral form (Fantinato et al., 2016), allowing for longer pollinator residence time and simultaneous pollinator presence. This in turn would prevent competitive exclusion events between Hymenoptera and Diptera.

Consistent with our third hypothesis, we showed that reproductive success of *L. narbonense* (quantified as fruit set) decreased significantly from the mainland to the water body. The negative relationship between fruit set and the distance from the mainland could be due to increasing pollen limitation caused by decreasing visitation rate of pollinators observed from the mainland to the water body. In a previous study, Garibaldi et al. (2011) showed that plant reproductive success in crop fields was negatively related to the distance from natural and semi-natural habitats, that serve as sources of wild pollinators.

Although the relationship between the visitation rate of pollinators and distance from the mainland was also negative for *G. pannonica*, no significant relationship was found between its reproductive success and distance from the mainland. A possible explanation for this could be that *G. pannonica* is a facultatively allogamous species. Self-compatibility is a common reproductive strategy in plant species that occur in areas where pollinators are scarce or have fluctuating populations (Kalisz et al. 2004), suggesting that *G. pannonica* may show such an adaptation in response to the variable distribution of pollinators in saltmarshes.

## 5. Conclusions

In addressing issues related to the dispersal of pollinators in the landscape matrix and their distribution among patches of suitable habitat, it is hypothesised that spatial patterns of floral diversity and abundance ultimately determine pollinator distribution. We have found that pollinator distribution in saltmarshes depends more on proximity to the mainland than on floral abundance. Floral abundance did not affect pollinator richness or visitation rates to flowering plants, nor did it affect reproductive success of target species, i.e., the function of pollination itself. From the perspective of island biogeography theory, our study may suggest that patches of suitable habitat are more likely to be colonised near the mainland than far away, and that the permeability of the landscape matrix depends not only on the movement ability but also on the feeding and reproductive behaviour of pollinators. More generally, our results suggest that the presence of patches of floral resources surrounded by a matrix of unsuitable habitat, do not necessarily ensure the maintenance of pollinators. Rather, they suggest that the degree of isolation of patches of suitable habitat is the critical factor in the distribution of pollinators that should be considered to improve the permeability of the landscape matrix to pollinators.

### Author Contributions

**Edy Fantinato:** Conceptualization, Methodology, Formal analysis, Supervision, Writing - Original Draft, Writing - Review & Editing **Sebastiano Favarin:** Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing **Gabriella Buffa:** Writing - Original Draft, Writing - Review & Editing

### Declaration of interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Nothing to declare.

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Table 1. Recorded pollinator species. For each species, the relative order, the maximum distance reached from the mainland (m) and the number of visits to *Limonium narbonense* and *Galatella pannonica* are reported.

Abbreviations: Hym = Hymenoptera; Dip = Diptera; Lep = Lepidoptera; Hem = Hemiptera.

Pollinator species	Order	Maximum distance recorded (m)	Number of visits to <i>L. narbonense</i>	Number of visits to <i>G. pannonica</i>
<i>Apis mellifera</i>	Hym	570.7	429	642
<i>Bombus pascuorum</i>	Hym	45.9	1	3
<i>Ceratina cyanea</i>	Hym	13.5	3	0
<i>Cerceris sabulosa</i>	Hym	95.9	1	0
<i>Colletes</i> sp.	Hym	493.1	14	31
<i>Cremnops desertor</i>	Hym	415.2	0	1
<i>Epeolus cruciger</i>	Hym	17.8	1	7
<i>Halictidae</i> sp.	Hym	177.8	1	0
<i>Halictus</i> sp.	Hym	280.4	0	8
<i>Halictus scabiosae</i>	Hym	17.8	1	1
<i>Halictus subauratus</i>	Hym	40.8	2	0
<i>Hoplitis</i> sp.	Hym	358.3	0	16
<i>Hedychrum nobile</i>	Hym	12.3	0	1
<i>Hylaeus</i> sp.	Hym	28.3	0	2
<i>Lasioglossum nigripes</i>	Hym	254.1	1	9
<i>Lasioglossum</i> sp.	Hym	227.5	0	1
<i>Megachile pilidens</i>	Hym	50.0	2	0
<i>Philanthus triangulum</i>	Hym	263.5	0	4
<i>Prionyx</i> sp.	Hym	5.1	2	0
<i>Pseudapis</i> sp.	Hym	100.7	1	0
<i>Sphecodes</i> sp.	Hym	16.6	1	0
<i>Vespa</i> sp.	Hym	311.5	3	0
<i>Chrysops italicus</i>	Dip	391.6	3	0
<i>Cucilidae</i> sp.	Dip	493.8	0	1
<i>Episyrphus balteatus</i>	Dip	570.7	102	37
<i>Eristalinus aeneus</i>	Dip	386.8	1	9
<i>Eristalinus sepulchralis</i>	Dip	262.9	3	1

<i>Eristalis tenax</i>	Dip	570.7	7	44
<i>Helophillus trivittatus</i>	Dip	533.0	16	32
<i>Lucilia caesar</i>	Dip	541.9	0	2
<i>Melanogaster</i> sp.	Dip	277.5	1	1
<i>Melanostoma</i> sp.	Dip	555.3	0	1
Muscidae sp.	Dip	98.9	1	2
<i>Nemotelus notatus</i>	Dip	493.8	20	10
<i>Phasia</i> sp.	Dip	462.1	0	3
<i>Sphaerophoria scripta</i>	Dip	386.8	6	35
<i>Syrpitta pipiens</i>	Dip	151.5	0	1
<i>Syrphidae</i> sp. 1	Dip	354.6	2	0
<i>Syrphidae</i> sp. 2	Dip	85.5	3	2
<i>Tephritis matricariae</i>	Dip	358.3	1	6
<i>Colias crocea</i>	Lep	163.2	0	5
<i>Cupido argiades</i>	Lep	3.4	2	0
<i>Hesperia comma</i>	Lep	28.3	0	3
<i>Lasiommata megera</i>	Lep	28.3	0	1
<i>Lycaena phlaeas</i>	Lep	45.9	0	1
<i>Macroglossum stellatarum</i>	Lep	0.9	0	1
<i>Pieris rapae</i>	Lep	5.3	0	1
<i>Polyommatus bellargus</i>	Lep	45.9	0	10
<i>Carpocoris purpureipennis</i>	Hem	100.7	1	0
<i>Hemiptera</i> sp. 1	Hem	104.4	1	0
<i>Hemiptera</i> sp. 2	Hem	316.6	9	0
<i>Nysius</i> sp.	Hem	225.1	1	0
Total number of visits	-	-	643	935

Table 2. Statistics of the relationships between pollinator species richness and visitation rate to *Limonium narbonense* and *Galatella pannonica* and distance from the mainland. Statistically significant results ( $p < 0.05$ ) are highlighted in bold.

Dependent variable	Independent variable	z-value	P	$\chi^2$
<i>Limonium narbonense</i>				
Species richness of pollinators	Distance from the mainland	-2.693	<b>0.006</b>	7.471
Visitation rate of pollinators	Distance from the mainland	-6.211	<b>&lt;0.001</b>	40.169
Species richness of Hymenoptera	Distance from the mainland	-2.839	<b>0.003</b>	8.533
Visitation rate of Hymenoptera	Distance from the mainland	-6.886	<b>&lt;0.001</b>	50.292
Species richness of Diptera	Distance from the mainland ^2	-1.415	0.143	2.144
Visitation rate of Diptera	Distance from the mainland ^2	-2.547	<b>0.007</b>	7.168
<i>Galatella pannonica</i>				
Species richness of pollinators	Distance from the mainland	-1.639	0.097	2.740
Visitation rate of pollinators	Distance from the mainland	-3.282	<b>&lt;0.001</b>	11.146
Species richness of Hymenoptera	Distance from the mainland	-0.940	0.343	0.899
Visitation rate of Hymenoptera	Distance from the mainland	-3.282	<b>&lt;0.001</b>	11.146
Species richness of Diptera	Distance from the mainland	0.469	0.640	0.218
Visitation rate of Diptera	Distance from the mainland	0.815	0.417	0.657

Table 3. Statistics of the relationships between the fruit set of *Limonium narbonense* and *Galatella pannonica* and distance from the mainland. Statistically significant results ( $p < 0.05$ ) are highlighted in bold.

Dependent variable	Independent variable	z-value	P	$\chi^2$
Fruit set of <i>L. narbonense</i>	Distance from the mainland	-2.857	<b>0.007</b>	7.086
Fruit set of <i>G. pannonica</i>	Distance from the mainland	0.653	0.516	0.420



Fig. 1 Map of the study area. The image above and to the left represents the map of the Venice Lagoon; the image above and to the right focuses on the Campalto saltmarshes with transects represented by black lines, while the image below represents a photograph of the study area focusing on the contact boundary between the vegetation of the sandbanks, mudflats and sandflats and the water body.



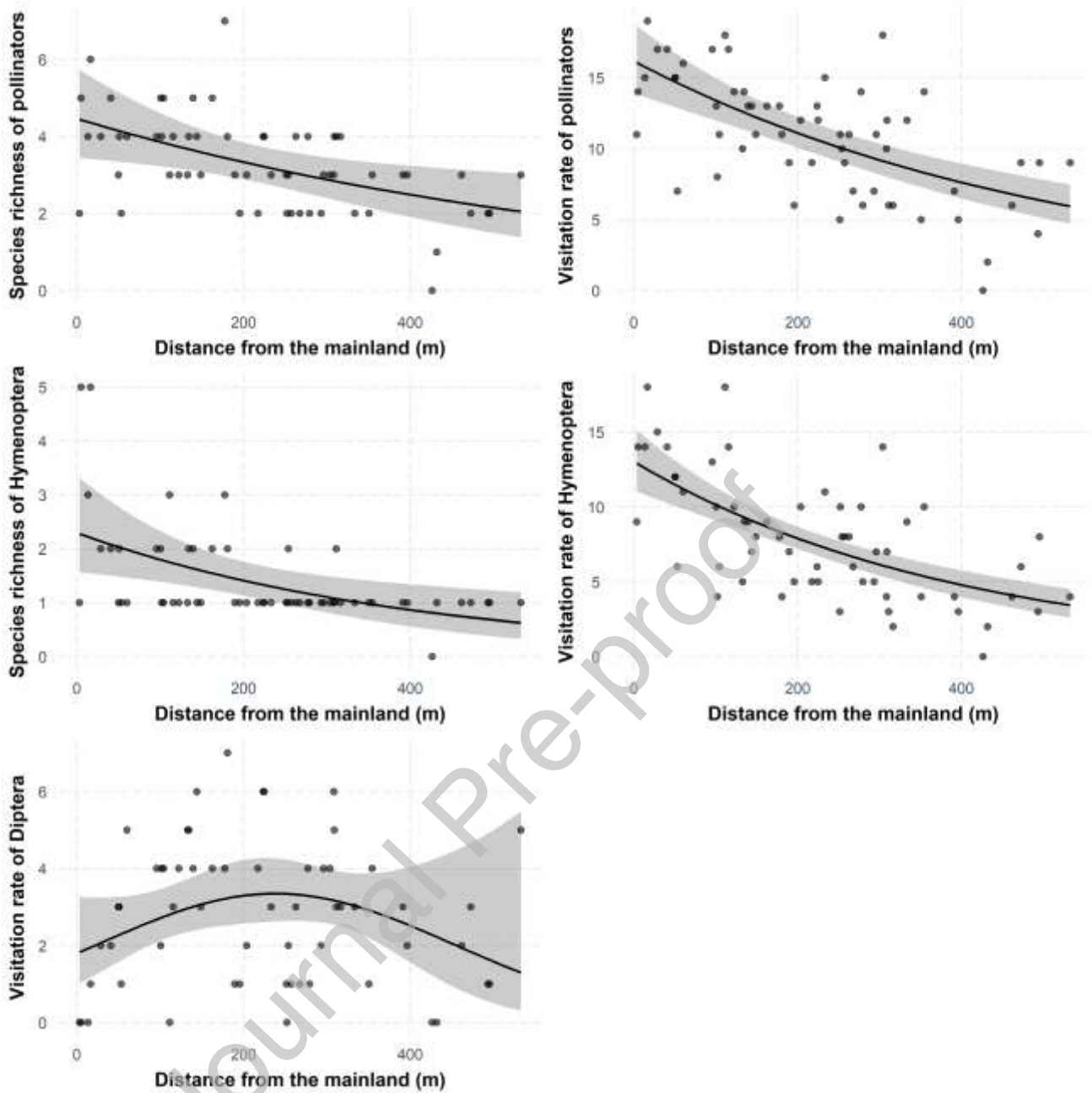


Fig. 2 Relationship between distance from the mainland (m) and species richness and visitation rate of all pollinators and Hymenoptera and visitation rate of Diptera, to *Limonium narbonense*. Lines represent the estimates of the Generalised Linear Models (GLMs). Black points are original data points, while the grey band represents 95% confidence interval around the regression line. Only significant results are shown in the figure.

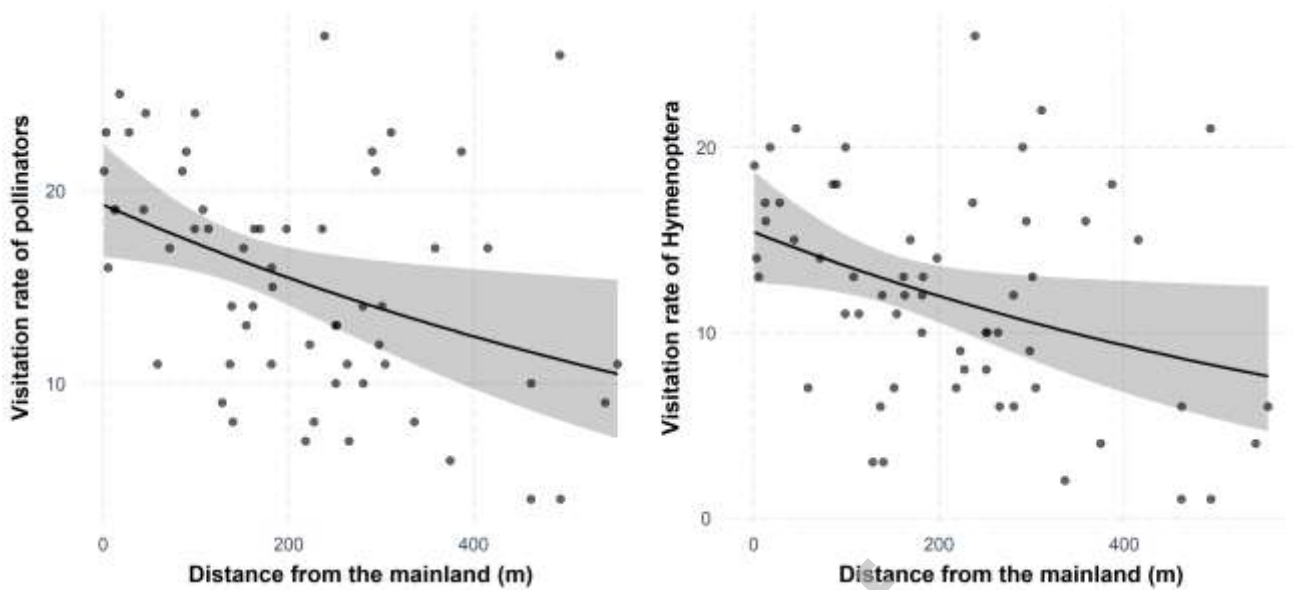


Fig. 3 Relationship between distance from the mainland (m) and visitation rate of all pollinators and Hymenoptera to *Galatella pannonica*. Lines represent the estimates of the Generalised Linear Models (GLMs). Black points are original data points, while the grey band represents 95% confidence interval around the regression line. Only significant results are shown in the figure.

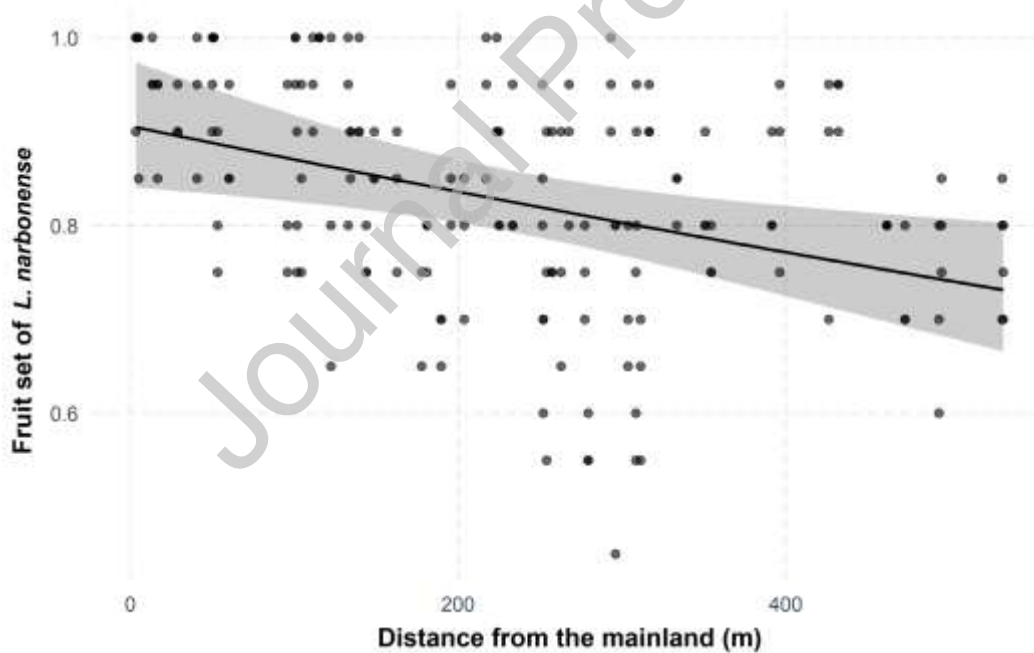


Fig. 4 Relationship between distance from the mainland (m) and the reproductive success (i.e., the fruit set) of *Limonium narbonense*. The line represents the estimate of the Generalised Linear Model (GLM). Black points are original data points, while the grey band represents 95% confidence interval around the regression line.