



The impact of (mass) tourism on coastal dune pollination networks

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ABSTRACT

Coastal dune ecosystems are increasingly threatened by the mass tourism phenomenon. Intense concentration of human activities and mass tourism are leading to coastal dune loss and fragmentation. Besides the loss and fragmentation of coastal dunes, mass tourism has considerably affected remnant natural areas. To prevent degradation of remnant natural areas, it is mandatory to understand whether, and under what conditions, tourism can be allowed. In the present study I addressed the problem by evaluating the impact of tourism on the structure and resilience of pollination networks in coastal dune ecosystems freely accessible to tourists. Pollination networks represent ecological community structure and depict interactions among species, providing the opportunity for a holistic assessment of ecosystem structure and functioning.

I conducted the study on coastal dune sites of the North Adriatic coast, with different levels of touristic pressure. I recorded pollination interactions together with descriptors of human disturbance along sea-inland transects. A moderate level of human disturbance was positively related to the richness of animal-pollinated plant and pollinator species. Besides species richness, the resilience of pollination networks was also highest at moderate disturbance. By assessing the impact of human disturbance on coastal dune ecosystems from the perspective of pollination interactions, evidence arises that moderate disturbance and long-term conservation of pollination networks of coastal dunes can co-exist. However, to achieve this goal, tourism should be regulated, and visitor access to coastal sites managed, so as to prevent intense human disturbance from compromising both the structure and function of coastal dune ecosystems.

1. Introduction

Human disturbance is threatening the integrity of ecosystems and their capability to withstand future environmental changes worldwide (Macdougall et al., 2013). Coastal dunes, including seashores, dune ridges and humid dune slacks, are ranked at the top of globally threatened ecosystems (Brown and McLachlan, 2002; EEA, 2009; Gigante et al., 2018). Growing demands for spare time and leisure activities have favored the real estate business along sandy coastlines, resulting in the replacement of sandy dune ecosystems with tourism-oriented settlements, infrastructures and facilities (Sperandii et al., 2018). Besides the loss and fragmentation of coastal dune areas (Malavasi et al., 2016), and the local extinction of plant and animal species (Barros, 2001; Del Vecchio et al., 2016), mass tourism has considerably affected remnant natural areas by thinning out vegetation caused by trampling and the diffusion of invasive and alien plant species (Santoro et al., 2012; Sperandii et al., 2019).

Trampling directly affects coastal dunes in two principal ways; by creating fine-scale fragmentation of plant communities through the formation of walking paths (Cole, 1995; Gallet and Roze, 2001), and by

contributing to foredune degradation, thus preventing the establishment of plant communities of semi-fixed and fixed dunes, which are highly sensitive to environmental disturbance factors like salt spray and sand blasting (Fenu et al., 2013). Moreover, in coastal dune ecosystems, diffusion of alien species is often encouraged by human trampling, which creates new, suitable habitats and contributes to the dispersal of their propagules (Silan et al., 2017). Alien species often trigger competitive interactions with native plants (Carboni, 2010). Specifically, they often prevent the establishment of native plants through the formation of dense populations (Del Vecchio et al., 2015), they transform local environmental morphological features (Isermann, 2008) and can alter the structure of trophic networks (e.g., pollination networks; Moragues and Traveset, 2005).

There is increasing concern about the decline of coastal dune ecosystems. This has initiated research aimed at understanding the capability of biotic communities to withstand destructive human activity which is the cause of the decline (Malavasi et al., 2018; Sperandii et al., 2018). However, though mounting evidence demonstrates that the resilience of terrestrial ecosystems strongly depends on the maintenance of ecological processes, their quantification and monitoring is still too

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infrequent. Indeed, unlike structural attributes of ecosystems, such as the presence, abundance and composition of species, the monitoring of ecological processes is more difficult because of the challenges involved in quantifying higher order emergent properties (Friberg et al., 2011).

In coastal dune ecosystems, animal-mediated pollination has a marked influence on dynamics and diversity of plant communities (Fantinato et al., 2018a). Moreover, coastal dunes are a hotspot for a number of highly habitat-specialized pollinator species (especially Hymenoptera), many of which find in sandy sediments a suitable substrate for nesting (Cane, 1991).

Understanding the relationship between species of two different trophic levels, which reciprocally influence each other, is of great importance for the conservation of their populations and the maintenance of ecosystem's resilience over time (Fantinato et al., 2018b, 2019a). Nowadays, pollination systems are under increasing threat of human-induced extinction due to the same factors that threaten conservation of coastal dune ecosystems: land use change, habitat loss and fragmentation, and invasions of non-native plants and animals (Kearns et al., 1998).

In the last decade, the resilience of pollination systems to human-induced extinction has been largely addressed through the use of the network approach (Fantinato et al., 2019b). Pollination networks not only represent ecological community structure but also depict energy or material flows between species and provide the opportunity for a more holistic assessment of an essential ecosystem process. Some attributes of pollination networks (i.e., network connectance, selectiveness, nestedness and modularity) have found a wide application in the assessment of network resilience, in virtue of their ecological meaning and sensitivity to various forms of natural and anthropogenic disturbance (e.g., habitat loss, grazing, fire; Lázaro et al., 2016; Welts and Joern, 2018; Traveset et al., 2018). However, studies often come to contradictory conclusions (e.g., Moreira et al., 2015; Revilla et al., 2015) and the response of pollination networks to human disturbance has yet to be fully understood.

In light of these considerations, the current study is aimed at evaluating the impact of human disturbance on coastal dune pollination networks by answering the following questions: (i) does the richness of animal-pollinated plant and pollinator species show similar responses to human disturbance? (ii) does human disturbance affect the structure and resilience of coastal dune pollination networks? Moreover, since coastal dune ecosystems are characterized by a precise sequence of ecologically distinct plant communities, I tested (iii) whether human disturbance equally affects pollination interactions of the different communities.

2. Material and methods

2.1. Study sites

I conducted the study on coastal dune ecosystems of the North Adriatic coast (Italy). They consist of narrow, Holocene dunes, made by carbonate sediments of dolomitic origin (Buffa et al., 2005; Gamper et al., 2008). The annual average temperature is 13 °C and the annual average precipitation is 831.5 mm (Buffa et al., 2012). Plant communities that characterize coastal dune ecosystems of the North Adriatic coast follow a precise sequence from the seashore inland (Buffa et al., 2005; 2007; Del Vecchio et al., 2018; Gamper 2008; Sburlino et al., 2008, 2013). The sequence begins with the pioneer community dominated by therophytes of the drift line zone (*Salsola kali-Cakiletum maritima* Costa et Manzanet 1981), which is followed by the plant community of shifting dunes (*Echinophoro spinosae-Ammophiletum australis* (Br.-Bl. 1921) Géhu, Rivas-Martínez et Tüxen in Géhu 1975), dominated by *Ammophila arenaria* ssp. *australis* (Mabille) Laínz. Landwards, the coastal sequence includes perennial xerophilous grasslands of the semi-fixed dunes dominated by dwarf shrubs (*Tortulo-Scabiosetum* Pignatti 1952). Lastly, the sequence ends with the xerophilous

shrublands (*Viburno lantanae-Phillyrethum angustifoliae* Gamper, Filesi, Buffa et Sburlino 2008, *Erico carnae-Osyridetum albae* Gamper, Filesi, Buffa et Sburlino 2008), and the xerophilous woodlands of fixed dunes (*Vincetoxic-Quercetum ilicis* Gamper, Filesi, Buffa et Sburlino 2008).

In 2017, tourism along the North Adriatic coast registered > 21 million visitors (<https://www.istat.it/it/archivio/178670>; accessed 24 March 2019). Summer beach tourism is one of the main resources of the region (Bezzi and Fontolan, 2003) and tourism-oriented facilities show an average density of about 76.3/100 km (Buffa et al., 2012). The huge concentration of tourism-oriented facilities has severely fragmented the continuity of coastal dunes; however, remnant coastal dunes are still considered highly valuable from an ecological point of view.

2.2. Sampling plant-pollinator interactions

In the study area I chose seven sampling sites freely accessible to tourists and with different levels of touristic pressure: three at Vallecchia (45.619 N, 12.945 E), two at the Mort Lagoon (45.532 N, 12.735 E) and two at the Cavallino Peninsula (45.439 N, 12.453 E).

At the beginning of the blooming season (early April 2018), I placed 2 permanent belt transects (Hill et al., 2005; Del Vecchio et al., 2019) per sampling site. Belt transects consisted of adjacent plots of 4 m × 4 m starting from the vegetation of the drift line and proceeding inland until the edge of the xerophilous woodlands of fixed dunes. I placed transects according to a consistent scheme 250 m apart from each other (Fig. 1).

Along each transect, I identified land cover types, including plant communities and walking paths, based on the fine-scale habitat map (scale 1:500; deliverable of the European LIFE project LIFE16 IT/NAT/000589 REDUNE; <http://www.liferedune.it/>; consulted 16.05.2019).

In each adjacent plot (Fig. 1), I recorded the number of floral displays per animal-pollinated species during three surveys at the beginning, the peak and the end of the blooming season (late April, middle June and late July 2018, respectively; Fantinato et al., 2018a). Depending on the plant species, a floral display consisted of a single flower, a flowering head (e.g., *Pilosella piloselloides* (Vill.) Soják inflorescence) or a group of flowers appearing together in a recognizable visual unit (e.g., *Thymus pulegioides* L.; Hegland and Totland, 2005; Fantinato et al., 2016). Moreover, during each survey (for a total of 3 surveys), I recorded visiting pollinators in each adjacent plot by observing the number of interactions between each plant and pollinator species. I considered visitors to be pollinators if they made direct contact with the floral reproductive organs and visited the flower for > 1 s (Hegland and Totland, 2005). I monitored each adjacent plot for 14 min, split up into two 7-min sets distributed during two daily intervals (from 10 a.m. to 1 p.m. and from 1 p.m. to 4 p.m.) to ensure the observation of pollinators showing different daily periods of activity (Lázaro et al., 2016; Fantinato et al., 2017). Overall, I monitored pollination interactions for 6776 min, and identified plants and pollinators to species or morphospecies. Moreover, I attributed to each plant species its (i) hosting habitat, by comparing field observations with the existing literature (Buffa et al., 2005; 2007; Del Vecchio et al., 2018; Gamper et al., 2008; Sburlino et al., 2008, 2013; Table A1 in Appendix A) and (ii) origin (i.e., native vs. alien plant species), by following Celesti-Grapo et al. (2010; Table A1 in Appendix A).

2.3. Network parameters

Overall, I created 21 pollination matrices; each matrix included pollination interactions recorded in one sampling site during one survey (7 subsites × 3 surveys). I chose to organize pollination interactions in one matrix per survey to avoid the formation of impossible interactions through pollinator sharing between plant species that bloom in different periods (i.e., forbidden links; Olesen et al., 2010).

For each pollination matrix, I calculated the richness of animal-pollinated plant and pollinator species. Furthermore, I quantified four

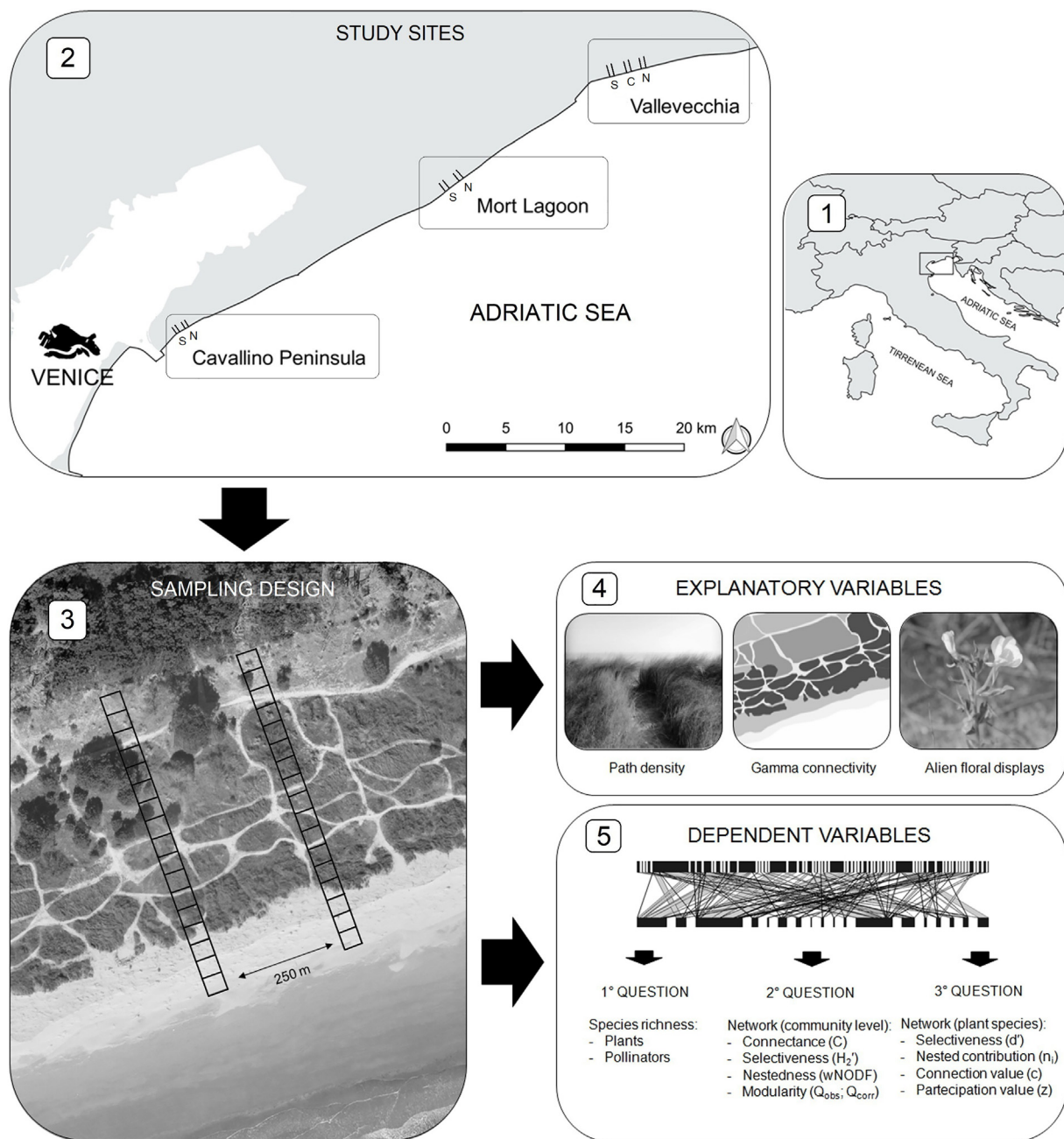


Fig. 1. Study workflow: (1) geographic location of the study area (2) sites, sampling sites (N, northern sampling site; C, central sampling site; S, southern sampling site) and belt transect distribution (transect are out of scale), (3) belt transect sampling design (out of scale), (4) independent variables chosen as descriptors of human disturbance and (5) dependent variables chosen as descriptors of the structure and resilience of pollination networks.

among the most used descriptors of the structure and resilience of pollination interactions by using the *networklevel* and *computeModules* functions in the R-based package *bipartite* (R version 3.4.3; *bipartite* package version 2.08; Dormann et al., 2008): network connectance (C; Dunne et al., 2002), network selectiveness (H_2' ; Blüthgen et al., 2006), weighted nestedness (wNODF; Galeano et al., 2009) and quantitative modularity (Q_{obs} ; Dormann and Strauss, 2014). Network connectance (Dunne et al., 2002) is the obtained proportion of possible interactions in a pollination network; while a high proportion of obtained interactions is generally expected to increase network resilience, empirical studies gave conflicting results (Helene et al., 2012), and the relationship between network connectance and resilience is still not clear. Network selectiveness (Blüthgen et al., 2006) is linked to the redundancy of interaction (i.e., partner sharing among species belonging

to the same trophic level), which influences the resilience of pollination networks by acting as a buffer against species loss. Weighted nestedness (Galeano et al., 2009), namely the tendency of specialist species to interact with generalist species, is thought to increase network resilience by decreasing the likelihood of extinction of specialist species (Vázquez and Aizen, 2004; Thebault and Fontaine, 2010). Finally, network modularity (Dormann and Strauss, 2014), namely the clustering of interactions between sub-groups of plants and pollinators, is expected to limit the spread of secondary extinctions through network modules (Tylianakis et al. 2010). Since observed modularity (Q_{obs}) strongly depends on network size, to ensure that the comparison of modularity was between the most unbiased estimates (Traveset et al., 2018), observed modularity was corrected for the mean of values resulting from 1000 randomized networks with identical margin totals as

the empirical network, using a model that maintained total number of interactions (Q_{corr} ; function null model; method r2d; R-based package *bipartite*; Schleuning et al., 2012; Martín González et al., 2010; Watts et al., 2016). Standardized z-scores ($z = [\text{observed} - \text{null mean}] / \text{null } \sigma$) were calculated for network connectance (C), selectiveness (H_2'), weighted nestedness (wNODF) and observed modularity (Q_{obs}) to test for significant differences from the null model distribution.

For each pollination matrix, I quantified the contribution of native plant species to the selective, nested and modular organization of pollination interactions by using a series of network parameters calculated at the species level. Specifically, I chose species selectiveness (d' ; Blüthgen et al., 2006), nested contribution (n_i ; Saavedra et al., 2011), and connection and participation value (c ; z ; Olesen et al., 2007). For a detailed description of the metrics see Table A1 in Appendix A.

2.4. Data analysis

For each transect, I summarized the impact of human disturbance on coastal dune ecosystems in three variables: (i) path density, (ii) gamma connectivity of land cover types intercepted by each transect based on the fine-scale habitat map (γ ; Forman and Godron, 1986), and (iii) relative abundance of alien floral displays (Table 1). I chose variables among the most informative descriptors of human disturbance on coastal dune ecosystems (Acosta et al., 2000; Buffa et al., 2012; Del Vecchio et al., 2015; Sperandii et al., 2018). For each transect, I calculated path density by counting the number of paths intercepted by the transect and dividing the result by the total length of the transect. Path density provides information on the diffusion of human disturbance and on the loss of habitat caused by path formation. The gamma connectivity index considers the number of links between different land cover-types, according to the formula, $\gamma = L / 3 (V - 2)$, where L is the number of observed links and $3 (V - 2)$ is the maximum possible number of links, counting the number of nodes present (V). The gamma connectivity index provides information on the degree of habitat fragmentation and ranges from 0 (only one land cover type can be observed) to 1 (every land cover-type is in contact with the others). In coastal dune ecosystems, where plant communities under favorable conservation status follow a precise sequence from the sea inland, low and high values of gamma connectivity are indicative of plant communities' homogenization or fragmentation, respectively, and affirm an overall inadequate conservation status (Acosta et al., 2000). Intermediate values of gamma connectivity represent the best spatial configuration of coastal plant communities, in which a neat sequence of communities from the sea inland can be observed (Buffa et al., 2012). Finally, I calculated the relative abundance of alien floral displays by dividing the number of floral displays of alien species by the total number of floral displays recorded in each subsite at each survey (Moragues and Traveset, 2005).

Since I calculated network properties for each sampling site, I averaged descriptors of human disturbance between each pair of adjacent-plot transects to allow for further analysis. Before assessing the effects of human disturbance on species richness and network parameters, I ran Variation Inflation Factor (VIF) analyses to identify collinear predictor variables that should be removed before data analyses

(Zuur et al., 2009). VIF values were smaller than two for all variables, thus none of the independent variables needed to be removed (Zuur et al., 2009).

I used separate generalized linear mixed models (GLMMs, package *lme4*; R version 3.4.3) to explore the effects of descriptors of human disturbance on richness of animal-pollinated plants and pollinators (1st study question) and on network parameters (2nd study question). Each model included descriptors of human disturbance as independent variables, (i) richness of animal-pollinated plants and (ii) pollinators, (iii) network connectance (C), (iv) selectiveness (H_2'), (v) weighted nestedness (wNODF), (vi) observed and (vii) corrected modularity (Q_{obs} ; Q_{corr}) as dependents and two random variables; i.e., site to avoid pseudoreplication (i.e., Vallecchia, Mort Lagoon and Cavallino Peninsula), and sampling site (nested within site). Moreover, I included the quadratic term of the path density and gamma connectivity in the GLMMs as independent variables to account for possible non-linear relationships. In the model in which the relationship between pollinator species richness and descriptors of human disturbance was calculated, I also included the richness of animal-pollinated plants as an independent variable. Indeed, numerous empirical studies reported a high influence of plant species richness on that of pollinators (e.g., Ebeling et al., 2008). I performed GLMMs by using: 1) Poisson distribution and log link functions for the richness of plant and pollinator species; 2) Gaussian distribution and log link function for the model of weighted nestedness (wNODF); and 3) gamma distribution and log link function for the network connectance (C), selectiveness (H_2') and both observed and corrected modularity (Q_{obs} ; Q_{corr}). I used network parameters calculated for each survey as replicates.

Then, I tested whether native plant species contribution to the structure of pollination networks changed with human disturbance by performing a series of GLMMs (3rd study question). I used separate models for different plant communities (i.e., three communities: pioneer community of the drift line, pioneer community of shifting dunes and xerophilous grasslands of semi-fixed dunes), by using values of species contribution to the network structure calculated per native plant species per sampling site, and at each survey, as replicates. In the models, I separately regressed species selectiveness (d'), nested contribution (n_i), as well as connection (c) and participation (z) values as dependent variables against independent variables describing human disturbance (and their quadratic term, in the case of path density and gamma connectivity), and by including site (i.e., Vallecchia, Mort Lagoon and Cavallino Peninsula) and species identity (included in the model as nested within site) as random factors. I analysed nested contribution (n_i) of native plants belonging to the pioneer community of shifting dunes by using a Gaussian distribution and log link function, while I used gamma distribution and log-link function for the rest of the parameters analysed regardless of the plant community type.

In each GLMM (including those at the overall network and species level), I followed the independent variable selection procedure for the mixed effects models (Zuur et al., 2010). At the beginning, the model selection procedure included all the independent variables (and their quadratic term, in the case of path density and gamma connectivity). Then, I used a stepwise backward selection procedure for the independent variables where, at each step, the variable with the highest

Table 1
General properties and descriptors of human disturbance of each sampling site.

Site	Sampling site	Mean transect length (m)	Mean gamma connectivity index	Mean number of walking paths	Mean path density (paths \times m ⁻¹)
Vallecchia	Northern	49.025	0.500	4.00	0.080
	Central	45.245	0.416	3.5	0.076
	Southern	63.790	0.366	5.0	0.080
Mort Lagoon	Northern	71.950	0.588	6.5	0.090
	Southern	144.075	0.550	6.5	0.043
Cavallino Peninsula	Northern	93.735	0.416	0.5	0.006
	Southern	248.530	0.476	2.5	0.009

P-value was left out until only terms with $P < 0.05$ remained in the model (Reitalu et al., 2014).

3. Results

Overall, I recorded 1173 interactions between 29 plant and 173 pollinator species. Plant species were all identified to species level and belonged to 15 families, the most speciose of which were Asteraceae (7 species; 24.14%), Fabaceae (4 species; 13.79%), Caryophyllaceae and Lamiaceae (both including 3 species; 10.34%), and Cystaceae (2 species; 6.90%). All the other families were represented by only one species (Table B1 in Appendix B). Among plant species, 24 were native, while five were alien: *Amorpha fruticosa* L., *Erigeron annuus* (L.) Desf., *Oenothera stueckii* Soldano, *Rosa rugosa* Thunb. and *Senecio inaequidens* DC. Alien species were recorded in all sampling sites, with *O. stueckii* being the most widespread (present in all sampling sites), followed by *A. fruticosa* (present in three sampling sites) and the remaining three (i.e., *E. annuus*, *R. rugosa* and *S. inaequidens*), which were present in only one sampling site. The pollinators recorded were all insects and belonged to four orders; 71 species and 35 morphospecies were Hymenoptera (61.27%), 15 species and 20 morphospecies Diptera (20.23%), 11 species and 6 morphospecies Coleoptera (9.83%) and 13 species and 2 morphospecies Lepidoptera (8.67%).

3.1. Effects of human disturbance on the richness of animal-pollinated plant and pollinator species

Both richness of animal-pollinated plant and pollinator species showed a significant unimodal relationship with the path density (Richness of animal-pollinated plants; $\chi^2 = 7.178$; d.f. = 1; $P = 0.003$; Richness of pollinator species; $\chi^2 = 4.322$; d.f. = 1; $P = 0.036$; Table 2; Fig. 2), reaching their maximum at moderate human disturbance.

3.2. Effects of human disturbance on network properties

Descriptors of network structure and resilience, i.e., network connectance (C), selectiveness (H_2'), weighted nestedness (wNODF) and modularity (Q_{obs}), were significantly different from random values during all the monitoring surveys (C; H_2' ; wNODF; Q_{obs} ; $P < 0.001$). Results of the GLMMs applied to descriptors of network structure and resilience showed a significant unimodal relationship between network

connectance (C), selectiveness (H_2') and weighted nestedness (wNODF) with path density (C; $\chi^2 = 3.955$; d.f. = 1; $P = 0.007$; H_2' ; $\chi^2 = 7.173$; d.f. = 1; $P = 0.002$; wNODF; $\chi^2 = 25.688$; d.f. = 1; $P < 0.0001$; Table 2; Fig. 2). Specifically, network connectance (C) and selectiveness (H_2'), reached their minimum at intermediate values of path density, proving that the obtained proportion of possible interactions between plants and pollinators (i.e., network connectance; C) was minimum, while the redundancy of interactions (i.e., network selectiveness, H_2') maximum at moderate human disturbance. Weighted nestedness (wNODF), namely the tendency of specialist species to interact with generalist species, reached its maximum at intermediate values of path density.

3.3. Effects of human disturbance on pollination interactions of native plant species belonging to different dune communities

Plant species belonging to different communities did not respond in the same way to human disturbance. The contribution of plant species of the pioneer community of the drift line to the network selectiveness (d'), nestedness (n_i) and modularity (c, z), was not significantly affected by human disturbance. On the contrary, nested contribution (n_i) and selectiveness (d') of plant species of shifting dunes and xerophilous grasslands of semi-fixed dunes varied significantly with human disturbance. Specifically, in the pioneer community of shifting dunes, the selectiveness (d') of plant species increased significantly as path density increased (d' ; $\chi^2 = 6.018$; d.f. = 1; $P = 0.0003$; Table 2; Fig. 2), revealing that under increasing human disturbance, pollinator sharing between plants diminishes. On the other hand, both in the pioneer community of shifting dunes and xerophilous grasslands of semi-fixed dunes, nested contribution (n_i) of plant species, namely the tendency of specialist plants to interact with generalist pollinators, reached its maximum at intermediate values of path density (pioneer community of shifting dunes; n_i ; $\chi^2 = 6.018$; d.f. = 1; $P = 0.0003$; xerophilous grasslands of semi-fixed dunes; n_i ; $\chi^2 = 6.423$; d.f. = 1; $P = 0.001$; Fig. 3) and of the gamma connectivity index (pioneer community of shifting dunes; γ ; $\chi^2 = 2.389$; d.f. = 1; $P = 0.042$; xerophilous grasslands of semi-fixed dunes; γ ; d.f. = 1; $\chi^2 = 4.284$; $P = 0.033$; Fig. 3). In other words, the nested contribution (n_i) of plant species was highest under moderate disturbance and where plant communities conserve a precise sequence from the sea inland.

Table 2

Species richness of animal-pollinated plants and pollinators, and quantitative descriptors of the structure and resilience of pollination interactions quantified in each subsite at each survey.

Site	Sampling site	Survey	Plant species richness	Pollinator species richness	Relative abundance of alien floral displays	C	H_2'	wNODF	Q_{obs}	Q_{corr}
Vallevecchia	Northern	1st	7	4	0.121	0.333	1.000	0.000	0.653	0.274
		2nd	6	28	0.000	0.208	0.658	9.482	0.503	0.160
		3rd	6	23	0.018	0.362	0.748	6.696	0.293	0.045
	Central	1st	10	18	0.119	0.158	0.667	1.724	0.713	0.284
		2nd	8	33	0.000	0.155	0.681	6.238	0.578	0.160
		3rd	10	32	0.011	0.165	0.670	5.446	0.607	0.185
	Southern	1st	9	22	0.000	0.183	0.616	7.143	0.537	0.160
		2nd	5	29	0.000	0.568	0.597	6.912	0.396	0.095
		3rd	7	16	0.012	0.333	0.690	4.505	0.473	0.218
Mort Lagoon	Northern	1st	3	5	0.000	0.500	1.000	0.000	0.219	0.031
		2nd	5	21	0.000	0.333	1.000	0.000	0.275	0.041
		3rd	5	29	0.000	0.250	1.000	0.000	0.632	0.234
	Southern	1st	9	29	0.223	0.164	0.428	7.593	0.539	0.143
		2nd	10	38	0.003	0.154	0.647	6.190	0.542	0.175
		3rd	11	28	0.050	0.138	0.682	10.688	0.398	0.170
Cavallino Peninsula	Northern	1st	8	13	0.004	0.208	0.605	4.859	0.627	0.356
		2nd	10	14	0.008	0.205	0.499	10.994	0.474	0.118
		3rd	9	29	0.065	0.293	0.602	12.235	0.084	−0.160
	Southern	1st	9	13	0.000	0.230	0.579	7.527	0.607	0.165
		2nd	13	25	0.212	0.138	0.605	4.859	0.627	0.251
		3rd	12	23	0.076	0.183	0.566	11.779	0.522	0.243

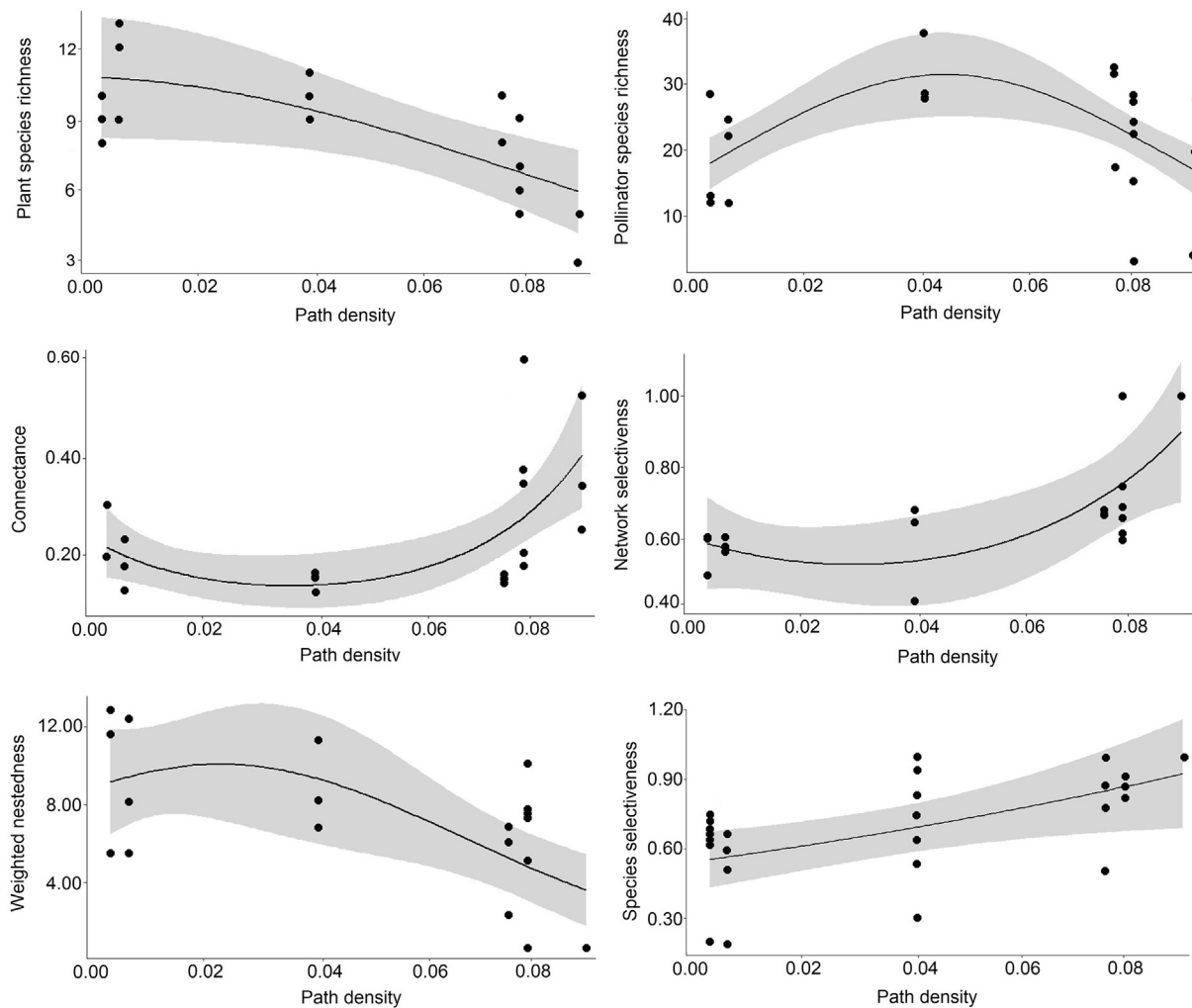


Fig. 2. Relationship between path density (paths m^{-1}) and the richness of animal-pollinated plant and pollinator species, network connectance (C), selectiveness (H_2'), weighted nestedness (wNODF) and selectiveness (d') of plant species of the pioneer community of shifting dune. Lines represent the estimates of the Generalized Linear Mixed Models (GLMM). Gray band represents 95% confidence interval around the regression line.

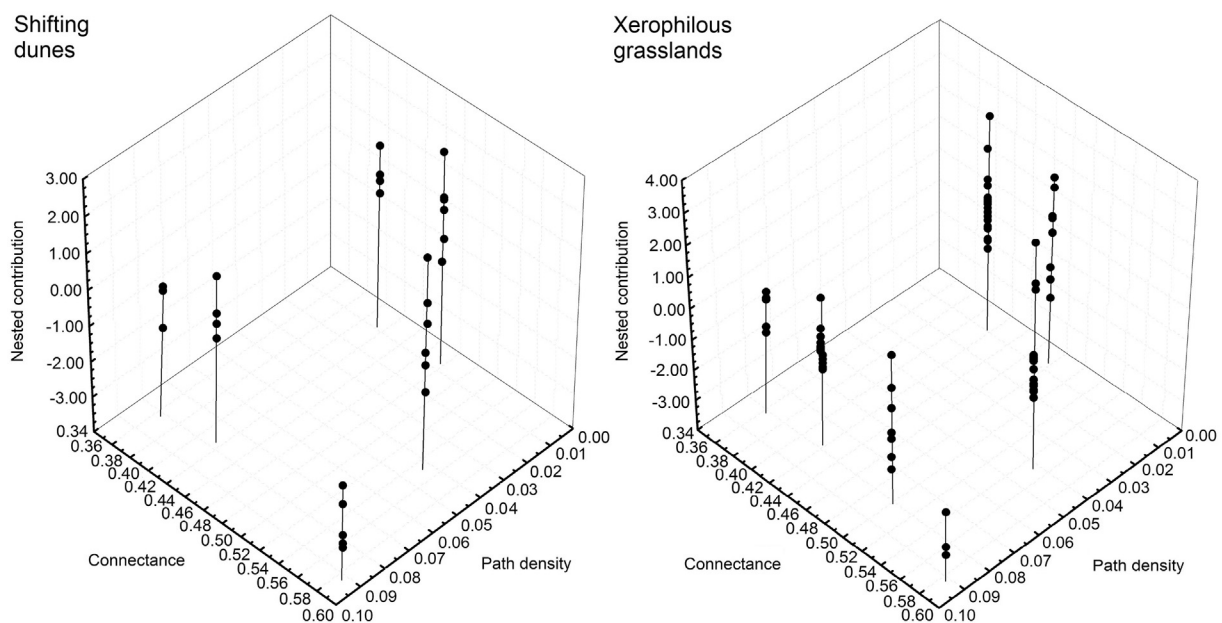


Fig. 3. Nested contribution of plant species of the community of shifting dunes and the xerophilous grasslands of semi-fixed dunes, as a function of path density and gamma connectivity.

4. Discussion

Human disturbance is considered one of the most important factors affecting remnant coastal dune ecosystems (Del Vecchio et al., 2015). Effects of human disturbance have widely been recognized in the local changes in species richness, with plants and terrestrial insects representing the most targeted groups of organisms (e.g., Comor et al., 2008; Buffa et al., 2018). The present study revealed that, besides species richness, human disturbance also influences the structure and resilience of coastal dune pollination networks.

4.1. Effects of human disturbance on the richness of animal-pollinated plant and pollinator species

The results from this study suggest that the response of the richness of animal-pollinated plants and pollinators depends on the intensity of human disturbance. Indeed, both the relationship between the richness of animal-pollinated plants and that of pollinators with path density were unimodal, in line with the intermediate disturbance hypothesis (Connell, 1978). According to this hypothesis the relationship between species richness and disturbance is hump-shaped, such that moderate disturbance maintains the highest species richness of plants and animals (Catford et al., 2012). In coastal dune ecosystems, the initial increase in species richness from human disturbance can result from the diffusion of therophytes and alien plant species (Pinna et al., 2019). However, under increasing human disturbance, alien species can rapidly establish competitive interactions with native plants, ultimately worsening local extinctions caused by direct habitat destruction (Carboni, 2010).

At the same time, moderate human disturbance might favor pollinator species by creating areas of bare sand and increasing micro-site diversification (Slaviero et al., 2016), eventually providing nesting sites to ground-nesting Hymenoptera (Murray et al., 2012; Vulliamy et al., 2006), which represent the dominant order of pollinators in sandy dune ecosystems (Fantinato et al., 2018a). However, given the high dependence of pollinator species on plants, a disturbance-induced reduction in floral resources may provoke competitive interactions between pollinators, possibly leading to the local exclusion of competitive weaker pollinator species (Schlindwein and Martins, 2000; Moron et al., 2009; Wojcik et al., 2018). This, in turn, might trigger negative feedback between plants and pollinators, thus reinforcing extinction events caused by direct habitat destruction.

4.2. Effects of human disturbance on network properties

As highlighted for the richness of pollinator species, the degree of network selectiveness (H_2') and weighted nestedness (wNODF), namely the degree of redundancy of interactions and the tendency of specialist species to interact with generalist species, were also unimodally related to path density. This result might be directly related to the influence that human disturbance has on the richness of pollinator species, because increasing the number of species may enhance the opportunities of interaction, ultimately improving the network resilience to perturbations (e.g., Vázquez et al., 2007, 2009). However, it is worth considering that, though general trends were unimodal, the highest values of selectiveness and the lowest values of weighted nestedness corresponded with extreme values of path density, namely with intense human disturbance (Fig. 2). These findings are in accordance with previous studies, which documented increases in network selectiveness and decreases in network nestedness under intense natural or anthropogenic disturbance (e.g., Moreira et al., 2015; Revilla et al., 2015; Traveset et al., 2018; Welti and Joern, 2018). High values of selectiveness, coupled with low values of nestedness, generally demonstrate an overall low network capability to maintain its structure and resilience in presence of local species extinctions (Bastolla et al., 2009). In particular, the likelihood of extinction of specialist species is expected

to increase and the structure of the overall network of pollination interactions to be much more prone to collapse (Vázquez and Aizen, 2004; Thebault and Fontaine, 2010).

Interestingly, the lowest values of network connectance (C), namely the obtained proportion of possible interactions between plant and pollinators, coincided with intermediate values of path density. While a high network connectance has often been considered as an indicator of resilience, according to Heleno et al. (2012) caution should be taken when interpreting connectance on its own. Indeed, given the intimate and negative relationship between species richness and connectance (Olesen and Jordano, 2002), the observed relationship might reflect differences in the richness of species among networks rather than the response of coastal dune pollination networks to human disturbance.

Though findings of the present study proved that human disturbance can significantly affect coastal dune species richness and pollination networks in different ways, no relationship could be detected between descriptors of pollination networks and the relative abundance of alien floral displays. Among indirect effects of human disturbance, invasions of alien plant species have been highlighted to severely threaten plant communities of coastal dunes (e.g., Carranza et al., 2012). Moreover, animal-pollinated alien plant species have often been considered as potential competitors of native species, and many studies have proven that alien plant species may have significant effects on the pollination outcome of the native ones, because they rapidly insinuate themselves into existing pollination networks (e.g., Morales and Traveset, 2009). In the present study, the relative abundance of alien floral displays explained neither variations in species richness, nor in descriptors of network structure and resilience, suggesting that alien plant species might have little impact on the network of pollination interactions. Indeed, the two most frequent alien plant species recorded in surveyed transects, i.e., *O. stuechii* and *A. fruticosa*, the first predominantly autogamous (Cecere et al., 2012), the second highly specialized for bees, and especially for *Apis mellifera* (L., 1758), thus poorly interconnected with the other species involved in coastal dune pollination networks.

4.3. Effects of human disturbance on pollination interactions of native plant species belonging to different dune communities

Differences in plant species response to human disturbance emerged when different communities were considered. Plant species of the pioneer community of shifting dunes were the most affected by human disturbance, showing an increasing degree of selectiveness (d'), namely the exclusiveness of a species partner spectrum, as path density increased. Moreover, in both the pioneer community of shifting dunes and xerophilous grasslands of semi-fixed dunes, nested contribution (n_i) of plant species, namely the tendency of specialist plants to interact with generalist pollinators, was unimodally related to path density and the gamma connectivity. As highlighted by the general trends of network selectiveness (H_2') and weighted nestedness (wNODF), a higher richness of pollinators at moderate levels of human disturbance, might improve the chances for each plant species to widen their spectrum of pollinators and to share pollinators with the other plant species, thus improving their contribution to the nested organization of interactions (Bastolla et al., 2009). Besides path density, the spatial configuration of plant communities, quantified through the gamma connectivity index (γ), significantly affected the nested contribution of plant species. The unimodal relationship observed between nested contribution and the gamma connectivity index indicates that both fragmentation and homogenization of plant communities can affect plant species contribution to the nested structure of pollination networks. In this regard, several features of the pollination ecology of plants can be affected by changes in the spatial configuration of plant communities. According to Xiao et al. (2016) these may include shifts and/or contractions in the blooming periods, and changes in the indirect pollination interactions with co-occurring plant species. Such changes can, in turn, alter the

contribution of plant species to the structure of pollination networks.

Interestingly, the contribution of plant species of the pioneer community of the drift line to the structure and resilience of pollination networks seemed not to be affected by human disturbance. It is reasonable to hypothesize that the low susceptibility of plant species of the drift line to human disturbance might be due to their natural adaptation to drastic landscape changes, either in composition or in configuration (Malavasi et al., 2018), and to their high tolerance to the environmental disturbance factors which, indeed, characterize the drift line (Del Vecchio et al., 2019).

5. Conclusions

By focusing on pollination interactions, the present study proved that intense human disturbance can significantly affect both the structure and functioning of coastal dune ecosystems, by causing the local extinction of plant and pollinator species and the simplification of pollination networks. However, results indicate that moderate human disturbance might have positive effects on coastal dune pollination networks. This result is not surprising, since it is not the human disturbance per se that exerts positive effects, rather the rejuvenation effect that it might have on local communities. Indeed, moderate disturbance might contribute to increased microsite diversification, and create suitable habitats for ground nesting pollinators.

By assessing the impact of human disturbance on coastal dune ecosystems from the perspective of pollination interactions, evidence arises that moderate disturbance and long-term conservation of coastal dune pollination networks can co-exist. However, in order to achieve this goal, tourism should be regulated, and visitor access to coastal sites managed, so as to prevent intense human disturbance from compromising both the structure and function of coastal dune ecosystems.

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Declaration of Competing Interest

Nothing to declare.

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