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Patterns of Seed Dispersal in Coastal Dune Plant Communities

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Abstract: Seed dispersal is a key determinant of species distribution, although it is still unclear how it contributes to species assembly in plant communities. We linked patterns of seed dispersal to coexisting species to investigate the role of dispersal in the species assembly process. We focused on 19 species coexisting in a foredune plant community, classified as "foredune foundation species", "semi-fixed dune species," and "alien species". The number of seeds dispersed by the 19 species was monitored monthly in 25 plots for 12 months. Then we compared both dispersal strategies and dispersal phenology among the species. Foredune foundation species, species of the semi-fixed dune, and alien species used the same dispersal strategies, with the exception of hemerochory, which was prevalently used by alien species. The three groups of species differentiated the dispersal season: semi-fixed dune species and alien species were early and late dispersers, respectively (spring vs. late summer), while foredune foundation species dispersed seeds in summer. Seasonal differentiation in seed dispersal may play a more important role in the species assembly process than dispersal vectors. Shifts in seasonality due to climate change may influence the timing of seed dispersal and provide species with different colonization opportunities.

Keywords: dispersal phenology; dispersal vectors; species coexistence; species colonization; seed traits

1. Introduction

Seed dispersal mechanisms allow plants to colonize other sites, even far away from the mother plant [1,2]. By influencing species colonization ability, seed dispersal plays a key role in determining species distribution patterns [3], metapopulation dynamics [4], and species composition in plant communities [5–7]. Moreover, by providing plants a chance to reproduce from seeds, seed dispersal supports gene variability in populations, thereby contributing to making populations more resistant and resilient to environmental changes [8].

Overall, it is often possible to identify dominant dispersal strategies in plant communities [9,10]. The adoption of similar dispersal strategies among coexisting species, i.e., trait overlap [11], can be particularly evident when the availability and abundance of given dispersal vectors constrain species to adopt the same strategies [12,13]. For example, plant communities occurring on the boundary between water and land host many hydrochorous species, whose seeds have adapted to flotation for survival when soaked [7,14,15], while wind-dispersed seeds prevail in open communities formed by herbs and grasses [9]. According to such findings, we may expect that in environments characterized by marked abiotic constraints ("environmental filters" [16]), the adoption of the same dispersal strategies (trait overlap) may promote successful species entering plant communities.

Although dominant dispersal strategies can be found in given plant communities, patterns of trait segregation (i.e., species that have different dispersal strategies) can also be observed among coexisting species. The use of different dispersal strategies has been related to species traits as growth form (e.g., in neotropical high altitude forest trees prevalently use zoochory, while herbs autochory [17]), or to species taxonomy (taxonomically related species have more similar strategies than taxonomically distant species [18]).

Patterns of trait overlapping or segregation can be detected not only in the dispersal strategies but also in the dispersal phenology. Indeed, species have been observed to disperse seeds in different periods of the year to match the seasonality of dispersal vectors, such as the migratory periods of birds, and of climatic variables, such as precipitation patterns [17,19]. Differentiating seed dispersal phenology can also enable germination to occur during the best season for seedling survival [20]. Moreover, Del Vecchio et al. (2021) [21] recently suggested that a segregated pattern of the germination niche may represent a mechanism for a species to enter a plant community by using different spatial or temporal niches during plant establishment.

Likewise, the use of different dispersal strategies or phenology may represent a mechanism for a given species to enter established plant communities [6,22]. However, links between dispersal and germination, as well as the contribution of seed dispersal to the species assembly process, are still unclear [2,5,23,24]. Since changes in the dispersal patterns may have implications on the species composition and structure of plant communities [23], elucidating the contribution of dispersal to species coexistence can significantly improve our capacity to predict plant communities' outcomes to changing environments.

In this work, we analyzed seed dispersal patterns in a foredune plant community to explore the link between seed dispersal mechanisms and the species coexisting in the target plant community. We then analyzed both dispersal strategies and dispersal phenology to investigate if the relationships between the two variables contributed to explaining species coexistence. Specifically, we analyzed if coexisting species: (i) use similar or different dispersal strategies; (ii) have different lengths of the dispersal period; and (iii) have overlapped or segregated dispersal phenology.

In coastal systems, plant communities are adjacent to each other so that up to 6–7 different plant communities can be found in a limited space, even of the order of magnitude of 100–200 m [25,26]. Since, in such a limited space, seeds are assumed to move easily from one plant community to another, coastal dune plant communities can be considered non-dispersal-limited, thereby representing ideal systems for the purpose of our research.

2. Materials and Methods

The research was carried out along the coasts of the Veneto region, in the SAC "Penisola del Cavallino: biotopi litoranei" (site code: IT3250003), a 15 km long stretch of beach near Venice. Although the area is characterized by intense touristic pressure, it hosts patches where the turnover of plant communities along the sea-inland gradient is complete (vegetation zonation [27,28]), ranging from pioneer plant communities on the strandline zone to woody scrubs and forests on the fixed dunes [29].

The sampling focused on 19 species coexisting in the foredune (Supplementary Materials, Table S1; see also the "Results" Section 3), previously defined by Del Vecchio et al. (2021) [21] from a database of about 500 plots. The target species were categorized [21] according to their distribution and abundance along the sea-inland gradient as: (i) "foredune foundation species" (n= 9), which almost exclusively occur in the foredune; (ii) "semi-fixed dune species" (n = 5), which occur more frequently in the adjacent semi-fixed dune but can be found in the foredune; "alien species" (n = 5), which occur in both foredune and semi-fixed dunes. Alien species were identified according to Galasso et al. (2018) [30].

The 19 species were monitored monthly in 25 plots of 2 × 2 m (Table S1). The number of plots was set according to an abundance-weighted sampling design so that the least abundant species had a representative number of measures while a higher number of measures was recorded for the most abundant species. We counted the number of ripe dispersal units (hereafter "seeds") borne by each species from October 2019 to October 2020. Ripe dispersal units were defined according to the standard protocol of the phenological development stages of plants [31]. In June 2020, we recorded the percentage cover of each species in each plot according to a 1–10 cover rank scale [32]. Then, for each species in each month, we calculated the number of seeds per m^2 by scaling the number of seeds per species by their respective cover percentage. Such standardization was made to avoid

biases in the values of the number of seeds per species due to species size or species density in the sampling plot.

We associated dispersal strategies with each species. Data were retrieved from the LEDA trait database [33] and included the categories listed in Table 1.

Table 1. Description of the analyzed dispersal strategies.

Dispersal Strategies	Vector	Description/Seed Morphology
Agochory	Human activities	The vector of transmission, in this case, is human activities (e.g., agriculture). Seeds of species adopting this strategy exploit anthropogenic means such as operating and/or agricultural machinery, truckloads, or ships
Anemochory	Wind	Plants produce light seeds, often with thin expansions to favor dispersal by wind
Autochory	Autonomous dispersal (no vector)	Plants simply drop seeds on the ground or hurl them through explosive mechanisms (in this case, the strategy is called "bolochory"). Autochory has the advantage of being independent of biotic or abiotic vectors, although the extent of dispersal is not very far from the mother plant
Chamaechory	Wind	When the individual reaches senescence, the aerial portion detaches itself from the roots and rolls away. The plant tends to have a rounded shape, which allows it to roll for considerable distances
Hemerochory	Humans and domestic animals	In this case, the transmission vector is humans. This strategy is similar to zoochory and allows seeds to attach themselves to shoes and clothes or domestic animals in order to be transported; this strategy is also long-range, as humans also move hundreds of kilometers
Nautochory	Water	It occurs through water (e.g., marine currents, run-offs, rivers, and canals). The fruits produced have to be able to float and survive in water for a long time without damaging the seeds
Zoochory	Animals	It occurs with the help of the most diverse species, such as birds, insects, worms, and mammals, above all, when the seeds remain attached to their hairy bodies. Fruits can be eaten by animals as well; in this case, they ought to be fragrant and attractive

To compare the duration of the dispersal period for each species, we measured the seed dispersal temporal niche breath by using the evenness index (J). In this way, we analyzed whether seed dispersal of the target species was evenly distributed over time (wide niche, long dispersal period) or it had peaks during a given period of the year (narrow niche, short dispersal period). Values of J near 1 (even distribution) indicate that the species do not have a preferential period for dispersal (i.e., dispersal can occur over a long period, even throughout the year), while values of J near 0 (dominance) indicate that the species have a peak of dispersal in a given period of the year.

Data Analyses

To explore the dispersal strategies used by the target species, we calculated the dispersal spectrum of the foredune plant community. Specifically, since many species implemented more than one strategy (e.g., *Cakile maritima* subsp. *maritima*, which implemented chamaechory and nautochory), we calculated the ratio between the sum of species using a particular dispersal strategy over the sum of all the strategies considered (i.e., the sum of the strategies was higher than the number of species). Differences in the use of dispersal strategies among foredune foundation species, species of the semi-fixed dunes, and alien species were investigated by the PERMANOVA test, followed by the post hoc Tukey test.

To investigate differences in the duration of the dispersal period among foredune foundation species, species of the semi-fixed dune, and alien species, we used the ANOVA test, setting the evenness index as the dependent variable and the group of species as the factor (factor with 3 levels). ANOVA assumptions were assessed by the Shapiro test.

Similarly, to investigate differences in the phenology of the dispersal period among foredune foundation species, species of the semi-fixed dune, and alien species, we used a GLM for Gamma distribution, using the number of dispersed seeds per month as the dependent variable, and the group of species, the month in which seeds were dispersed and their interaction as factors. We used such a model because ANOVA assumptions were not met even after data transformations, while the distribution of the dependent variable fitted a gamma distribution.

All analyses were performed in the R statistical framework [34].

3. Results

Overall, the main dispersal strategies were nautochory and zoochory (27% each; Figure 1; Table 2), followed by autochory and hemerochory. Dispersal strategies were evenly distributed among foredune foundation species, species of the semi-fixed dune, and alien species, with the exception of hemerochory, which was mainly used by alien species with respect to the foredune foundation species (permanova test; F = 2.48; $p = 0.04$; post hoc Tukey test between foredune foundation species and alien species: $p = 0.03$).
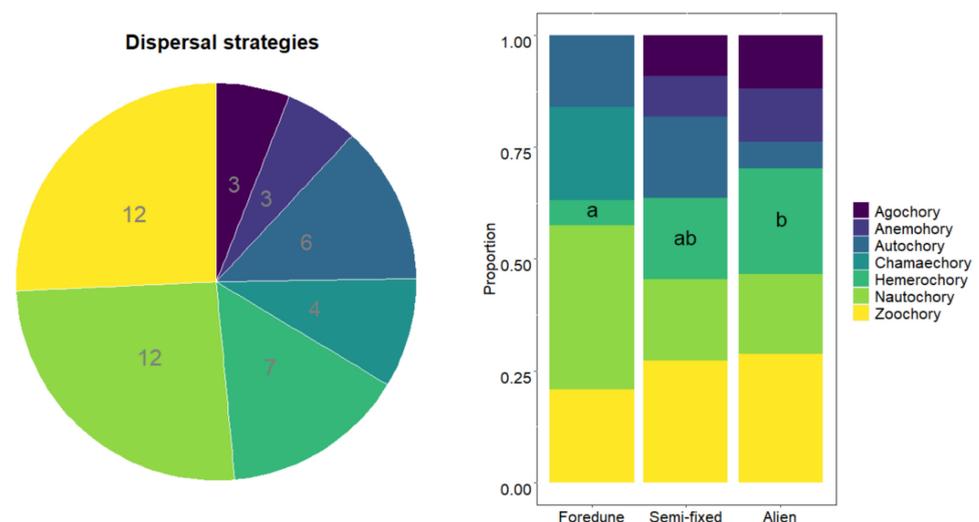

Figure 1. Pie chart representing the percentage of the dispersal spectrum of the target species, and bar plot representing the distributions of dispersal strategies across foredune foundation species, species of the semi-fixed dune, and alien species. The numbers shown in the pie chart refer to the number of species using a given dispersal strategy. The different letters in the bar plot indicate significant differences from the post hoc Tukey tests. The strategies that did not differ among the groups (i.e., among foredune foundation species, species of the semi-fixed dune, and alien species) have no letters. A color-blind-friendly palette was used for the figure [35,36].

Table 2. Number and type of dispersal strategies used by each species. The dispersal strategies were retrieved from the LEDA trait database [33], with the exception of *Cenchrus longispinus*, *Cyperus capitatus*, *Echinophora spinosa*, and *Medicago littoralis*, which were not present in the database. For these species, the dispersal strategies were defined by field observation. The last column shows the Evenness index, calculated to estimate the temporal niche breath of each species. Species nomenclature follows Bartolucci et al. (2018) [37].

	Species	Number of Strategies	Dispersal Strategy	Evenness Index
Foredune foundation species	*Cakile maritima* subsp. *maritima*	2	Chamaechory; Nautochory	0.57
	Calamagrostis arenaria subsp. *arundinacea*	2	Nautochory; Zoochory	0.55
	Calystegia soldanella	1	Nautochory	0.28
	Echinophora spinosa	1	Chamaechory	0.09
	Elymus farctus	2	Nautochory; Zoochory	0.55
	Eryngium maritimum	5	Autochory; Chamaechory; Hemerochory; Nautochory; Zoochory	0.31
	Euphorbia paralias	2	Autochory; Nautochory	0.54
	Euphorbia peplis	1	Autochory	0.34
	Salsola tragus	3	Chamaechory; Nautochory; Zoochory	0.16
Semi-fixed dune	*Festuca fasciculata*	3	Anemochory; Nautochory; Zoochory	0.44
	Cyperus capitatus	1	Autochory	0.44
	Hypochaeris radicata	4	Agochory; Hemerochory; Nautochory; Zoochory	0.39
	Medicago littoralis	2	Hemerochory; Zoochory	0.18
	Silene colorata	1	Autochory	0.37
Alien	*Ambrosia psilostachya*	2	Hemerochory; Zoochory	0.28
	Cenchrus longispinus	2	Hemerochory; Zoochory	0.46
	Erigeron canadensis	5	Agochory; Anemochory; Hemerochory; Nautochory; Zoochory	0.39
	Oenothera stucchii	6	Agochory; Anemochory; Autochory; Hemerochory; Nautochory; Zoochory	0.47
	Xanthium orientale	2	Nautochory; Zoochory	0.69

Foredune foundation species, species of the semi-fixed dune, and alien species had similar duration of the dispersal period (ANOVA test: F = 0.556; *p* = 0.584). The duration of seed dispersal was of 3–4 months for each group of species (Figure 2).

The three groups of species had different dispersal phenology (Table 3; Figure 2). Foredune foundation species dispersed seeds in summer and early autumn (approximately from July to October, with a peak in August), species of the semi-fixed dune in late spring and summer (approximately from May to July, with a peak in May), while alien species dispersed seeds in late summer and autumn (approximately from September to November, with a peak in October).

Table 3. Summary table of the GLM to test differences in the dispersal phenology among the 3 groups of species (foredune foundation species, species of the semi-fixed dune, and alien species).

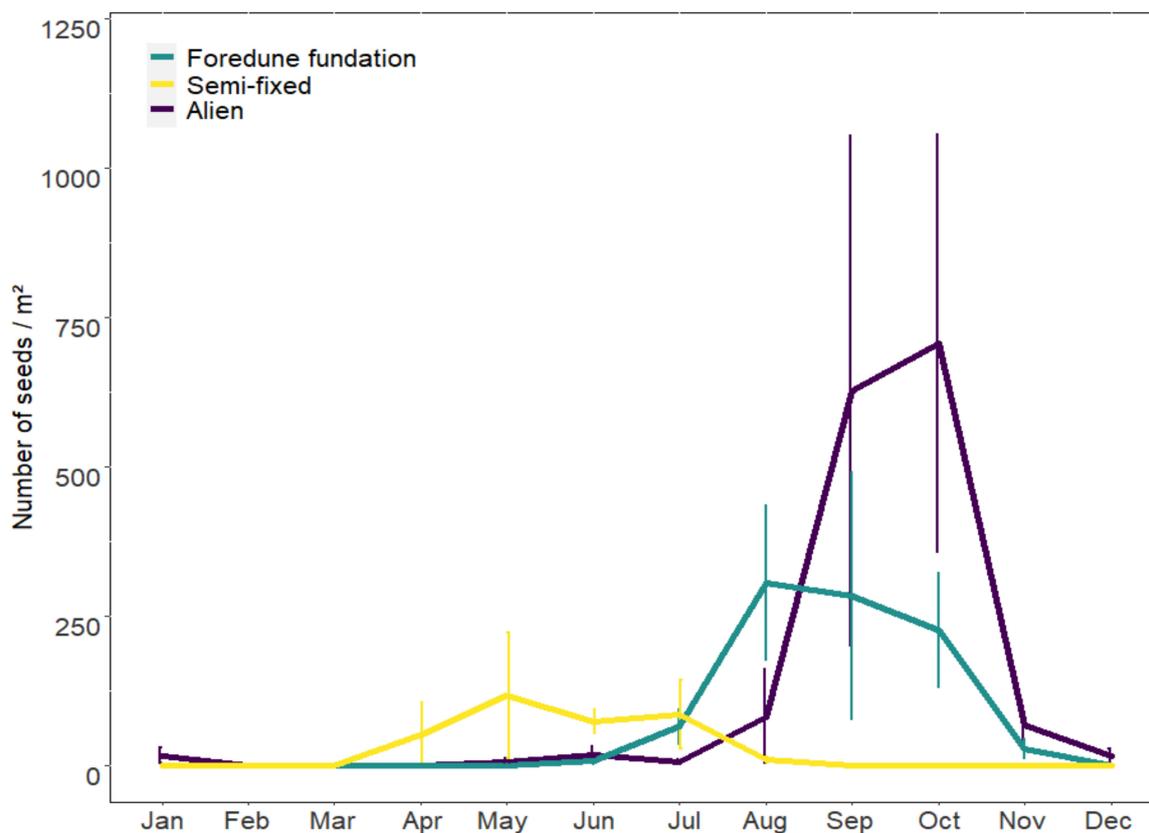|	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL	227	4043.6			
Month	11	1301.34	216	2742.3	<0.0001
Species group	2	149.15	214	2593.2	<0.0001
Month × Species group	22	1217.79	192	1375.4	<0.0001

Figure 2. Dispersal phenology of the target species, showing the number of seeds dispersed for each species over the year. Bars represent Standard Error.

4. Discussion

The species occurring in the foredune used several dispersal strategies. Foredune foundation species, species of the semi-fixed dune, and alien species share the dispersal strategies but differentiate their dispersal phenology.

Although we found two dominant strategies, i.e., nautochory and zoochory, the majority of the species were polychorous, i.e., they relied on more than one dispersal vector. This can be seen as a "bet hedging" strategy [38–40], i.e., a strategy that allows species to live in spatially and temporally variable environments, such as coastal dunes. In these environments, seedling survival is hampered by many limiting factors such as drought, substrate mobility, and salinity [41,42]. The use of different dispersal strategies allows plants to spread the risk among seeds that reach different sites, thereby providing a higher chance for them to find suitable conditions for establishment. While mechanisms that allow seeds to move over a considerable distance from the mother plant (e.g., anemochory, nautochory [43]) play a major role in determining processes such as population spread, the flow of individuals between populations, and the colonization of unoccupied habitats [44], the adoption of short-distance dispersal strategy such as autochory [45], represents a conservative strategy that often shapes the dynamics of local populations and communities. Indeed, seeds dispersed by autochory fall near the mother plant, within a distance of about 10 m [45], thus ensuring that seeds fall in appropriate germination sites where adult plants have already established and grown [46]. In coastal dunes, similar environmental conditions are found at the same distance from the sea, along belts parallel to the coastline, while very different conditions are found at increasing distances from the sea, in an orthogonal direction to the coastline [28,42]. Accordingly, seeds dispersed too far from the mother plant along the sea-inland direction may fall in unsuitable sites, such as water, or in inland plant communities, where they may not be able to establish. We may speculate that in coastal

dunes, the use of short-distance dispersal coupled with vector-mediated long-distance dispersal (occurring in species such as *Eryngium maritimum*, or *Euphorbia paralias*) could be an ideal mechanism to ensure the permanence over time of the local population and the colonization of other possibly suitable sites.

Hemerochory was the only strategy that differed among the three analyzed groups of species, being more common in alien species. This result supports previous evidence that humans are a preferential vector that provides alien species a chance of colonization by overcoming natural barriers to seed dispersal [29,47–49]. Besides polychory, species also shared the duration of the dispersal period, suggesting an overlapped pattern in seed dispersal traits. The overlapped pattern may indicate that such dispersal mechanisms are required, or at least provide species with an advantage in colonizing the foredune. However, they segregated as far as the dispersal phenology was concerned, particularly the peak of dispersal, which occurred in different seasons. This segregation in the dispersal phenology may favor species coexistence by avoiding excessive competition during seed production: undoubtedly, the production of seeds, which precedes the dispersion, has a high metabolic cost and requires a large amount of resources [50,51]. Dispersing seeds in different seasons may limit competition for the same resources.

The segregation in dispersal phenology that we found may also limit competition during seedling establishment, being coordinated with the germination niche. Indeed, foredune foundation species, semi-fixed dune species, and alien species proved to have different germination niches [21]. The different dispersal phenology may enhance species to match different suitable seasons for germination, thereby maximizing species germination success.

The use of different phenology was already observed for alien species with respect to native species in arid and semi-arid environments in terms of germination and leaf emergence [52]. It was explained as a mechanism that enables alien species to persist in the invaded communities by matching the most favorable period for survival when alien species lack adaptations to cope with high stress [52]. Interestingly, alien species had early phenology compared to the species of the invaded community, while we observed late phenology (i.e., they dispersed seeds after the majority of the other native species present in the community). In the foredune plant community, late phenology may still favor the establishment of alien species by the exploitation of favorable environmental conditions during autumn, which is a suitable season for seedling establishment and growth in Mediterranean coastal dunes [53].

5. Conclusions

Our research contributed to advancing the knowledge on dispersal strategies in dune systems and understanding the role of seed dispersal in plant communities. By analyzing mechanisms of seed dispersal at the community level, our research suggests that seasonal differentiation in seed dispersal, and, specifically, segregation in dispersal phenology, may play a crucial role in the species assembly process rather than dispersal vectors. In this context, shifts in seasonality due to climate change may influence the timing of seed dispersal and provide species with different colonization opportunities. This study suggests that the analysis of phenological aspects of plants may significantly contribute to explaining the processes involved in species assemblage and coexistence. A clearer understanding of the drivers of species coexistence will, in turn, contribute to planning adequate conservation actions aimed at preserving the integrity of plant communities, thereby counteracting biodiversity loss.

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