Functional seed traits and germination patterns predict species coexistence in NE Mediterranean foredune communities

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- **Background and Aims** The structure of plant communities, which is based on species abundance ratios, is closely linked to ecosystem functionality. Seed germination niche plays a major role in shaping plant communities, although it has often been neglected when explaining species coexistence. The aim of this work is to link the seed germination niche to community ecology, investigating how functional seed traits contribute to species coexistence.

- **Methods** Species selection was based on a database of 504 vegetation surveys from the Veneto coast (Italy). Through cluster analysis we identified the foredune community and selected all of its 19 plant species. By using the "Phi coefficient" and frequency values, species were pooled in different categories (foundation species, accidental species of the semi-fixed dune, and aliens), then the 19 species were grouped according to their germination responses to temperature and photoperiod through cluster analyses. For each germination cluster we investigated germination trends against temperature and photoperiod by using GLMMs.

- **Key Results** We identified four germination strategies: (1) high germination at all tested conditions ("high-germinating"); (2) high germination at warm temperatures in the dark ("dark warm-cued"); (3) high germination at warm temperatures in the light ("light warm-cued"); and (4) low germination, regardless of conditions ("low-germinating"). Foredune foundation species showed a narrow germination niche, being "low-germinating" or "dark warm-cued". Annual species of semi-fixed dunes were "high-germinating", while alien species were the only members of the "light warm-cued" cluster.

- **Conclusions** Our research suggests that different categories of species have dissimilar seed germination niches, which contributes to explaining their coexistence. Climatic events, such as rising temperature, could alter germination patterns, favoring seed regeneration of certain categories (i.e. alien and semi-fixed dune species) at the expense of others (i.e. foundation species, pivotal to ecosystem functioning), hence potentially altering the plant community structure.

INTRODUCTION

Healthy and functioning coastal ecosystems provide an important supporting service by protecting and buffering inland areas from environmental hazards, such as soil erosion and saltwater intrusion (Hanley *et al.*, 2020). The provision of their invaluable benefits and services depends on plant community integrity and resilience to withstand environmental changes, since species composition and their abundance ratio are regulators of ecosystem processes and of the final service that they provide (Cardinale *et al.*, 2012; Mace *et al.*, 2012; Pascual *et al.*, 2017). However, species within a plant community do not equally contribute to ecosystem functioning (Lefcheck *et al.*, 2015). Foredune plant communities, constrained by limiting abiotic factors such as sand burial, flooding and incoherent substrate, are often composed of few species, assembled in a marked dominant hierarchy, where few dominant species are followed by other of lower abundance (i.e., occasional or accidental species; Prisco *et al.*, 2012; Del Vecchio *et al.*, 2019). The dominant species also represent foundation species, i.e. those which form the structure of the community, create suitable ecological conditions for other species, contribute to the function of ecosystem and to the stabilization of ecosystem processes (Ellison *et al.*, 2005; Fantinato *et al.*, 2018a). Foredune foundation species are those which trap sand and fix sediments, increase soil elevation, and build the dune system, thereby making the entire system able to attenuate waves, keep up with sea level rise, protect the inland against flooding, and prevent the erosion of the shoreline (Borsje *et al.*, 2011; de Battisti and Griffin, 2020). Due to this pivotal functional role, any event that could hinder their occurrence is expected to have severe implications for the integrity of the entire community and dune system's function.

Understanding the processes that drive the assemblage of species into communities has long been a major challenge for ecologists (Keddy, 1992; de Bello *et al.*, 2012; Funk *et al.*, 2017). Trait-based ecology has made significant advances to explain species occurrence and coexistence within communities, describing how and when plant species use the resources, and analysing their competition/facilitation relationships (Funk *et al.*, 2017; Fantinato *et al.*, 2018b; Chelli *et al.*, 2019). However, although plant communities are shaped by environmental factors that act on all phases of a plant life cycle (Grubb, 1977), research efforts mainly focused on adult plants (Jiménez-Alfaro *et al.*,

2016; Saatkamp *et al.*, 2019; Del Vecchio *et al.*, 2020). Indeed, early stages of a plant life history are very sensitive to environmental factors, and any event that can impair plant's development, such as global warming, will influence population dynamics, and species coexistence within communities (Walck *et al.*, 2011; Fernández-Pascual *et al.*, 2017). Accordingly, a growing number of studies are demonstrating that including seed traits in community ecology studies contributes to a better understanding of plant communities' assembly (e.g. Poschlod *et al.*, 2013; Larson and Funk, 2016; Fernández-Pascual *et al.*, 2017; Tudela-Isanta *et al.*, 2018; Rosbakh *et al.*, 2019). Seed mass and shape are traits related to seed dispersal ability, their longevity in the soil seed bank, as well as to the vigour of seedling (Thompson *et al.*, 1993; Cerabolini *et al.*, 2003; Jiménez-Alfaro *et al.*, 2016). The analysis of these seed traits could help clarify colonization patterns and species persistence within communities over time. Other functional seed traits, such as germination timing, could reveal how species share resources over time during the early stages of their development (Gioria *et al.*, 2018).

In harsh environments, such as coastal dunes or those characterized by marked seasonality, seeds have a narrow phenological window of opportunity to germinate in order to ensure the most favourable period for seedling survival and establishment (Baskin and Baskin, 2014). To overcome adverse conditions, species often have complex requirements that regulate seed germination timing. In temperate areas, to prevent emergence during periods of water stress in summer, which is particularly critical in the southern Mediterranean areas of Europe, species are adapted to germinate under cold temperature in autumn/winter (Thanos *et al.*, 1991; Ne'eman and Goubitz, 2000; Fenner and Thompson, 2005; Picciau *et al.*, 2019). Similarly, photoinhibition is a common adaptation in arid environments, and represents a strategy to prevent seed germination in the light, i.e. at or near the soil surface, to avoid desiccation during seedling development (Carta *et al.*, 2017). On the contrary, in northern European coasts, where summer drought is not a constraint, adaptation to germinate under warm temperature in spring/summer prevents emergence during severe winters, characterized by frost and more frequent extreme events (e.g. storms, flooding; Fenner and Thompson, 2005). In coastal environments, salinity tolerance is another important driver of seed germination and seedling establishment phenology (Lum and Barton, 2020). Although seeds of species located near the

coastline are more tolerant to saline conditions than inland species, they tend to germinate when salt concentration in the soil has the lowest values, in correspondence or immediately after rainfall seasons (Del Vecchio *et al.*, 2020).

Finally, seed dormancy, which is a complex mechanism related to several environmental and physiological signals, is a widespread strategy in harsh environments to fine regulating the germination timing (Baskin and Baskin 2014) as for example, allowing species to overwinter and germinate in spring, as well as to avoid germination when soil salinity is too high, or when high temperature is excessive for seedling survival (Baskin and Baskin 2014).

The seed trait approach can also provide a conceptual framework to predict possible scenarios of species coexistence under different ecological conditions (Walck *et al.*, 2011). The identification of the range of cues (i.e. the germination niche) to which seeds are able to germinate may elucidate species adaptation ability to environmental conditions. Species with a wide seed germination niche are more likely at least to germinate if environmental conditions change while species which depend on specific cues have less chance to withstand environmental changes during germination (Walck *et al.*, 2011; Finch *et al.*, 2019). Any event that could hinder germination may have severe implications on the structure of the community, and consequently impact on the functions that it provides. Although dune plant species often have clonal reproduction (Maun, 2009), their regeneration from seeds remains fundamental to maintain population variability and resilience over time (Cochrane *et al.*, 2015). In this context, the need to analyse seed traits to better understand and predict patterns of species coexistence in plant communities become crucial, as evidenced in recent researches (e.g. E-Vojtkó *et al.*, 2020; Phartyal *et al.*, 2020).

Therefore, the main aim of this study was to analyse the structure of a foredune plant community from a functional seed trait, including germination patterns, perspective. Our hypothesis is that the analysis of the germination pattern of species in a community may reveal species coexistence processes and assembly rules driven by functional seed traits. We assumed that these traits are related to the structure of plant communities, thus we expected that foredune foundation species and

accidental species had different morphological seed traits and germination requirements, which may contribute to explain their coexistence.

MATERIALS AND METHODS

Study area and species selection

Vegetation surveys were carried out in coastal dune systems along Veneto coast (Italy, NE Mediterranean, between Tagliamento and Po rivers, about 120 km long). Although the study area is in the Mediterranean basin, it lacks the summer drought typical of the Mediterranean climate (Buffa *et al.*, 2007; Del Vecchio *et al.*, 2018a). The mean temperature of the hottest months (June - August) is of ca. 23 °C, while precipitation is almost evenly distributed across the year. No aridity periods are observed (Supplementary data Figure S1).

Species selection was based on multivariate analyses. We used a database of 504 plots x 155 species including all communities of the coastal zonation, surveyed from 2012 to 2017, by the Plant Ecology research group of Ca' Foscari University of Venice. Through a cluster analysis (Bray-Curtis distance, beta-flexible method, on presence-absence data; Pc-Ord 5.1; McCune and Mefford, 2006) we identified three groups of plots. Then, for each group of plots, we distinguished the "diagnostic" species, i.e. species which preferably occur in a given plant community (Chytrý *et al.*, 2002). To statistically identify the diagnostic species, we assigned to each species measures of concentration of occurrence in each group of plots, i.e. fidelity and frequency values. As fidelity value, we used the "Phi coefficient" (setting the Fisher exact test at 0.01) calculated by using the Juice software (Tichý, 2002). The maximum value of the "Phi coefficient" is 100 and indicates that a species occurs in all plots of a given group and is absent elsewhere. The "Phi coefficient" is not assigned to those species that have no diagnostic capacity, i.e. equally occurring in all groups of plots. Frequency was expressed as the percentage of plots in which a species was found in a given group, with respect to the total number of plots. This procedure allowed us to define the three groups of plots as "foredune",

"semi-fixed dune", and "fixed dune". The foredune group was made of 60 plots x 19 species. Cluster dendrogram and the map of the study area are provided in Supplementary data Figure S1.

To analyse the structure of the foredune community, we selected all the 19 species listed in the 60 plots of the foredune. Within this pool of species, we identified "alien" species, according to Celesti-Grapow *et al.* (2010). Successively we classified as foundation species those with Phi values and the highest frequency in the foredune group of plots (alien excluded). Species which had Phi values or high frequency in the other groups of plots (semi-fixed dune or fixed dune) were classified as accidental, i.e. species that occur more frequently in other communities, but were accidentally found in the foredune (Table 1). Moreover, we assigned to each of the 19 species information on their life cycle (annual, biennial, or perennial), growth form (Cornelissen *et al.*, 2013), main reproductive strategy (i.e. by seeds, vegetative, or both; BiolFlor database, Klotz *et al.*, 2002), and on the month in which seeds were collected.

Seed collection

Seeds of the 19 species were collected along Veneto coasts (in the study area described above; Supplementary data Figure S1) in spring and summer 2018, at the time of natural dispersal according to the species phenology (Supplementary data Table S2). Species nomenclature follows POWO (2019). For each species, seeds were collected from approximately 100 randomly selected plants, in the site where, according to our database, the species showed the maximum abundance value. Afterwards, seeds were manually cleaned and sent to Wakehurst Place – Royal Botanic Gardens, Kew (UK) in October 2018, were they were stored at 15°C and 15% RH, until the seed germination experiments were carried out (from the end of October 2018 to the end of February 2019).

Morphological seed traits

For each species, we measured individual seed mass by an average of 10 replicates of five (or 10 when they were very small) seeds. Moreover, we assessed the shape of the dispersal unit on 15 replicates, measuring seed length, width and depth, under a stereoscope (Leica 205c, Leica Microsystems, UK) equipped with a digital camera (DMC5400, Leica Microsystems, UK). To calculate the shape index, we standardized the three seed dimensions by dividing length, width and depth by length, so that length is the unity. Then we calculated the variance among the standardized length, width and depth (Thompson *et al.*, 1993). According to this formula, the shape index value ranges from 0 to 0.3, where 0 indicates spherical shapes and 0.3 cylindrical/flattened shapes. The dispersal units (seeds afterwards in the text) coincided with the seed for the majority of the species, except for *Cenchrus longispinus*, *Medicago littoralis* and *Xanthium strumarium* subsp. *strumarium*, for which they were fruits (Supplementary data Table S3).

Germination tests

Four replicates of 20 seeds each were sown in Petri dishes, on 1% agar-water solution. Seeds were incubated at a range of constant temperatures (5, 10, 15, 20, 25 °C), in both 12/12 h photoperiod (light treatment) and 24 h of constant darkness (dark treatment). Seeds were sown without any pre-treatment, with the exception of scarification for seeds with impermeable coat, verified by imbibition tests (*Ambrosia psilostachya, Calystegia soldanella* and *Medicago littoralis*). For the light treatment, germinated seeds were scored every other day, while, in the dark treatment, seeds were scored weekly in a darkroom, under safe green light. Tests were ended after 45 days of observations. Non-germinated seeds were cut to assess seed viability and to exclude possible empty seeds (cut test; Davis *et al.*, 2015), and the germination percentage was calculated as the final number of germinated seeds on the seeds sown in each dish (excluding empty seeds).

Data analyses

To explore phylogenetic relationships of traits among taxa, we generated a phylogenetic tree for the 19 species, by using Phylomatic (Webb and Donoghue, 2005), and the phylogenies provided by Zanne *et al.* (2014). We used the Blomberg's K (Blomberg *et al.*, 2003) to test for a phylogenetic signal in each morphological and germination trait (at each temperature and photoperiod regime; *phytools* R package; Revell, 2012). Blomberg's K evidenced no association between phylogeny and both, morphological and germination traits (K < 0.15 for most of the traits; p > 0.05 in all cases). Therefore, all further analyses were carried out without taking phylogeny into account.

To sort species according to their germination response, we used a cluster analysis (Euclidean distance, ward method) and ordination (PCA; Pc-Ord 5.1), with species as objects, and germination percentage at each temperature and photoperiod as variables (matrix of 19 species x 10 variables; to avoid that the row sum was equal to 0 in the main matrix, zero values were replaced with 0.01). Within each cluster, we investigated germination response to light and temperature by Generalized Linear Mixed Models (GLMMs) with binomial error distribution and logit link function, setting temperature and photoperiod as fixed factors and species as random factor (R Core Team, package lme4; Bates *et al.*, 2014).

Seed mass and shape were compared among clusters by using Permanova (9999 randomizations; Past software; Hammer *et al.*, 2001), followed by Post hoc Tukey test.

RESULTS

Within the 19 species evidenced by the cluster analysis for the foredune group of plots, we identified nine foundation species, five accidental species belonging to the semi-fixed dune, and five aliens (Table 1). No species were typical of the fixed dune. The foundation species included perennial species with rhizomes (*Calamagrostis arenaria*, *Calystegia soldanella*, *Echinophora spinosa*, *Eryngium maritimum*, *Euphorbia paralias, Thinopyrum junceum*) and annual species (*Cakile maritima*, *Euphorbia peplis, Salsola kali*). Within alien species, *Xanthium strumarium* subsp. *strumarium* and *Cenchrus longispinus* were mainly concentrated in the foredune system, *Oenothera*

stucchii and *Ambrosia psilostachya* in the semi-fixed dune system, while *Erigeron canadensis* was evenly distributed across the foredune and the semi-fixed dune systems.

The three categories of species differed in the time of seed collecting, being summer for foredune foundation species, spring and early summer for semi-fixed dune species, and late summer for alien species (Table 1). The majority of the species (42%) were "Erect leafy", i.e. with leaves concentrated in middle and/or top parts. Reproduction from seeds was the main reproductive strategy (63% of the species); only three species, *Calamagrostis arenaria*, *Cyperus capitatus*, and *Ambrosia psilostachya* reproduced mostly vegetatively, and rarely by seed (Table 1 and Supplementary data Figure S4).

Final germination results for each species are detailed in Supplementary data Table S3. Overall, seed germination was highly variable among species, ranging from 0 to 100% (Supplementary data Table S3). Species with high germination percentage (> 80%) and those with low percentage (< 20%) had consistent values across treatments, showing low standard deviation (between 0 and 10%, with the exception of *Hypochaeris radicata* and *Silene colorata*), while species with intermediate germination percentages (between 20 and 50%) had less uniform values and high standard deviations. The cut test revealed that non-germinated seeds were mostly viable (higher than 70% for the majority of the species).

The cluster analysis evidenced the clumping of the investigated species in three main Clusters according to their germination performance among temperature and photoperiod ("A", "B", "C", Fig. 1), with Cluster B divided into two subclusters, for a total of four Clusters. The majority of foredune foundation species were included in Cluster 1, with the exception of *Thinopyrum junceum* and *Salsola kali*, which were included in Cluster 2, and *Calystegia soldanella* in Cluster 4. Species of semi-fixed dunes were mainly included in Cluster 4, while alien species were for the most part included in Cluster 3. The solely aliens with different germination pattern were *Ambrosia psilostachya* and *Cenchrus longispinus*, which were included in Cluster 1 and 2, respectively.

GLMMs confirmed the pattern highlighted by the cluster analyses. In particular, GLMMs revealed that Cluster 1 included species with adaptation to high temperature and darkness, although the germination percentage was very low, being of ca. 6% averaged by all tested conditions (hereafter "low-germinating" Cluster; Fig 2; see Supplementary data Table S5 for the Summary table of GLMMs). Species of both Clusters 2 and 3 (which belonged to the Cluster "B") showed a positive trend with temperature and a significant interaction term "temperature x light". However, species of Cluster 2 had higher germination percentages in the dark than in light ("dark warm-cued"), while those of Cluster 3 showed higher germination in the light than in the dark ("light warm-cued"; Fig. 2; Supplementary data Table S5). Species of Cluster 4, although showing a significant interaction term "temperature x light", had very high germination at all tested conditions (higher than 80% across all treatments, hereafter "high-germinating"; Fig. 2; Supplementary data Table S5).

Seed mass had an average of 7.31 ± 10.49 mg (ranging from 3.23 ± 2.90 mg to 9.80 ± 17.53 mg among the Clusters), while the shape of the dispersal unit was 0.13 ± 0.22 (ranging from 0.05 ± 0.04 to 0.15 ± 0.12; Table 2; Supplementary data Table S3). The Clusters did not differ in their seed mass (Permanova test, 9999 randomizations; F=2.25; p=0.0763), while they showed a different shape of the dispersal unit (Permanova test, 9999 randomizations; F=7.636; p=0.0002). In particular, the shape of light warm-cued species (Cluster 3) was spherical, while those of the other Clusters was cylindrical or flattened (Post hoc Tukey test; p<0.001 only for the light warm-cued Cluster compared with all other Clusters). Table 2 summarizes seed mass and the shape of the dispersal unit for each Cluster (see Supplementary data Table S3 for mean values of each species).

DISCUSSION

Seed germination patterns

We identified different categories of species which coexist within the foredune community. The majority of the foundation species, which are those that contributed the most to the spatial configuration and species pool of the community, had a narrow or complex germination niche. Indeed, they failed to germinate or had a very low germination percentage ("low-germinating" species, Cluster 1). However, the high number of fresh non-germinated seeds suggests that seeds did not meet the germination requirements rather than a low initial seed quality. According to literature, about 60% on 116 investigated psammophyte species are reported to have physiological seed dormancy (Baskin and Baskin 2014). Within the species investigated in our study, physiological dormancy has been previously reported for seeds of *Calamagrostis arenaria* (Baskin and Baskin 2014), morhophysiological dormancy for *Eryngium maritimum* (and in other species of the Apiaceae family; Vandelook *et al.*, 2007; Nekajeva and Ievinsh 2013), and Nondeep Physiological Dormancy was reported within the genus *Euphorbia* (Cristaudo *et al.*, 2019). Indeed, we may hypothesize that such kinds of dormancy are responsible for the low germination percentage observed in our study for *Echinophora spinosa*, *Euphorbia paralias* and *Euphorbia peplis*. Consistently to our results, *Cakile maritima* has been reported to germinate without any pre-treatment (Fernández-Pascual *et al.*, 2017; Del Vecchio *et al.*, 2018b), although cold stratification enhanced its germination percentage (Fernández-Pascual *et al.*, 2017). While dormancy in *Ambrosia psilostachya* has not been classified, primary dormancy of other *Ambrosia* species (*A. artemisifolia*, *A. trifida* and *A. tenuifolia*) was broken by cold stratification and subsequent exposure to light, while their secondary dormancy was induced by dark and warm temperature (Montagnani *et al.*, 2017). Thus, for the species investigated in our research that failed to germinate or showed low germination values, the effect of dormancy breaking mechanism should be tested. Since this Cluster of species shed seeds mainly in summer, germination in spring after natural cold stratification during winter, or a combination of warm and

cold stratification, is likely to occur (Maun, 2009). Seedling emergence in spring, found for *Cakile maritima* (Davy *et al.*, 2006), *Eryngium maritimum* (Walmsley and Davy, 1997) and *Euphorbia paralias* (Ranwell, 1960), supports this hypothesis. Moreover, to understand the germination requirements of this Cluster of species, the effect of other temperature regimes, as fluctuating temperature, should be investigated. Indeed, *Cyperus capitatus* and *Silene colorata* were reported to germinate without any pre-treatment at the alternate temperature of 25/15°C (Salmeri and Trubia, 2019) and 20/15°C respectively (Benvenuti, 2016). Although dormancy breaking mechanisms for the species included in this Cluster remain to be investigated, by analysing seed germination without any pre-treatment and exposing seeds to the same conditions, our study allowed us to elucidate the basic germination requirements, discerning easy-germinating by complex-germinating species.

Other foredune foundation species (*Thinopyrum junceum* and *Salsola kali*), had higher germination in the dark at warm temperature ("dark warm-cued", Cluster 2), in the range of 20-25°C, which coincides with spring and summer temperature of the study area. This result contrasts those obtained in Mediterranean systems, where it has been observed that the germination niche is generally characterized by low temperature, in the range of 5-15 °C, that coincides with autumn, an adaptation to avoid seedling exposure to summer drought (Fenner and Thompson, 2005; Ne'eman and Goubitz, 2000; De Vitis *et al.*, 2014), although this pattern was not always confirmed (Mayfield *et al.*, 2014). In our case, the shift to warm temperatures could be explained by the lack of summer drought in the study area. However, it cannot be excluded that the shift in the temperature dimension of the germination niche in the foredune species may have been superimposed by fine-scale environmental constrains, which depend on the sea-inland ecological gradient. Being the most seaward-located, foredune plant communities are exposed to storms, over-washing, and flooding, which mainly occur in winter, and represent severe hazards for seedling survival (Fernández-Pascual *et al.*, 2017; Martínez and Psuty, 2004). Adaptation to darkness found for this Cluster of species suggests that seeds germinate when buried deeply in the sand, where moisture conditions are less limiting than at the substrate surface, thereby counteracting desiccation by this strategy (Thanos *et al.*, 1991; Fernández-Pascual *et al.*, 2017; Rajaniemi and Barrett, 2018). Thus, the germination of foredune

species is likely to occur in spring and summer, tuned by either possible cold stratification during winter as a requirement to brake dormancy (as hypothesized or found for some of the species included in the "low-germinating" Cluster) or by adaptation to warm temperature. This suggests that foredune species may share an "azonal" germination strategy, i.e. the germination is regulated by factors other than macroclimatic features which characterize the geographic areas; namely, regardless of the bioclimatic zone, germination in spring and summer represents a strategy to overcome storms and intense burial during winters, and to protect seedlings from drought during summer by germinating in darkness. On the contrary, germination in autumn observed for Mediterranean species (Fenner and Thompson, 2005; Ne'eman and Goubitz, 2000; De Vitis *et al.*, 2014), may represent the best strategy for seedling survival for landward located species (e.g. those of semi-fixed dunes), which are sheltered from the influence of the sea, as wave energy and flooding.

The third Cluster was represented by species with high germination at warm temperature in the light ("light warm-cued", Cluster 3). Interestingly, this Cluster only included alien species, that thus occupy a separate germination niche with respect to the other species of the foredune community. Alien species establishment has been often associated to "gap colonization" mechanisms (i.e. they establish and grow in vegetation gaps and open areas; Del Vecchio *et al.*, 2015). By using an ecological gap to germinate, we may hypothesize that alien species adopt not only spatial gaps, but also "temporal gaps", a mismatch in germination timing with respect to the invaded community. The possible exploitation of spatial and temporal gaps during germination may provide aliens a chance of establishment when and/or where other species are disadvantaged. In line with our results, successful establishment and invasion ability of alien species has been related not only to a different resource use strategy during the adult phase (Conti *et al.*, 2018), but also to a different germination niche (Gioria *et al.*, 2018). Furthermore, it would be interesting to compare the germination requirements of alien species both in their native and invaded distribution area to verify their robustness or plasticity, since flexible germination cues may be key traits that facilitate alien invasion in new environments (Wainwright and Cleland, 2013).

The species with the widest germination requirements, i.e. able to germinate at all tested conditions with high percentages ("high germinating", Group 4), were mainly those of semifixed dunes. It is worth noting, however, that among the semifixed dune species pool, only annual, also known as "ruderal" species (Grime, 1977; Prisco et al., 2012; Del Vecchio et al., 2019), which invest in a rapid growth and in sexual reproduction, have been found in the foredune community. Due to their "opportunistic" ecology, ruderal species are able to colonized different environments (Prisco et al., 2012; Silan et al., 2017); they often occupy clearings of perennial vegetation, have an ephemeral spring flowering, invest the resources in seed production, and withstand disturbance thanks to their ability to exploit temporarily favorable conditions (Grime, 1977). Our results suggest that their ability to successfully colonise different environments can also be related to their wide germination niche, i.e. the ability to germinate under a wide range of conditions. Thus, once gaps and open areas have been created, their coexistence in the foredune community is assured by their successful germination under several conditions, followed by the ability to use the resources in a short period of time.

Morphological seed traits

Seed mass did not differ among the four Clusters of species. Compared to the seed mass of species of other environments in Italy, the seed mass of the analyzed species could be classified as large (Cerabolini *et al.*, 2003). Indeed, on average it was comparable to that of species with the largest seed mass, as species of Mediterranean maquis and garigues (10.3 ± 13.1 mg) and temperate woodlands (5.7 ± 13.7mg; Cerabolini *et al.*, 2003), while species of alpine pastures and limestone prairies showed a smaller seed mass (1.5 ± 2.0 mg and 3.4 ± 5.9 mg, respectively; Cerabolini *et al.*, 2003). In dynamic environments, as sand dunes which are characterized by incoherent substrate and sand burial, large seeds have an advantage over small seeds because can emerge from greater depth, and generate larger seedlings, which have higher chance of establishment (Maun, 2009). Large seed mass and consequently the potential ability to germinate from great depth is in line with the lack of light requirement for seed germination (Carta *et al.*, 2017), a pattern that we found also for some

species analysed in our study. The shape of the dispersal unit was different only for alien species. Having a spherical shape, they have a higher probability to form a persistent seed bank with respect to the other species of the foredune community (Thompson *et al.*, 1993; Cerabolini *et al.*, 2003).

Winners and losers versus changing environmental conditions

Although field conditions might differ from laboratory-controlled conditions, our results provided insights on the estimated responses of the regeneration from seeds of each species category to changing environmental conditions. Our study evidenced a clear differentiation in the regeneration niche, which reflects different germination requirements across species categories and allows species coexistence under current conditions. Particularly interesting is the width of thermal window for seed germination and thermal stress resilience for the investigated species. The effects of a warming environment on plant reproduction cannot be reduced to absolute successful or unsuccessful germination, but it should be quantified in terms of changing rates and thresholds for the physiological process that underlie reproduction by seed, both before (e.g. seed mass and physiological dormancy) and after seed dispersal (e.g. seed germination phenology; Fernández-Pascual *et al.*, 2019).

Species with a wide germination niche, i.e. able to germinate under different conditions ("high germinating", Cluster 4), proved to have a broad environmental tolerance, and thus are expected to be less affected by a changed environmental scenario (Finch *et al.*, 2019). Similarly, species adapted to warm temperature ("light and dark warm-cued", Cluster 2 and 3) are expected to be buffered against rising temperature (e.g. by shifting the germination season), or even favoured by warmer temperature, if soil moisture is not limiting (Cochrane, 2019). Indeed, the component belonging to semi-fixed dune species and alien species, along with the few species of the foredune that could germinate without any pre-treatment will continue to reproduce from seed with trends similar to the current ones, suggesting a beneficial effect of increasing environmental temperatures on their reproduction by seed.

On the contrary, "low-germinating" species (Cluster 1) showed a complex germination and/or dormancy breaking requirements and need specific cues to germinate. In the field, germination requirements of dormant species are often fulfilled by seasonal changes, as exposure to cold winter temperature is followed by higher spring temperature, or exposure to warm summer temperature is followed by cooler autumn temperature (Finch-Savage and Leubner-Metzger, 2006). The reproduction by seed of those species which are particularly dependent on seasonal changes (e.g. mean temperature) and on environmental triggers for dormancy breaking (e.g. duration of winter; cold stratification), are thus expected to be hindered by climate change more than other species (Walck *et al.*, 2011; Parmesan and Hanley; 2015; Fernández-Pascual *et al.*, 2019). According to our analyses, the reproduction from seed of foredune foundation species, which mainly belong to the "low-germinating" Cluster, could therefore be the most affected by climate change.

It can be argued that several foredune species, and particularly foundation species such as *Calamagrostis arenaria*, rely on mechanisms of vegetative propagation that allow to counteract the lack of germination. However, although we can expect that the lack of germination in clonal species will not have direct effects on species abundance in a short period, it should be considered that reproduction form seeds is crucial to ensure population resilience through higher genetic variability, and species colonization capacity (i.e. the ability to move away from the mother plant, or to recover after individuals removal or damage). Thus, we cannot exclude that a long-lasting lack of reproduction from seeds may ultimately affect plant community structure and function.

CONCLUSION

We analyzed germination patterns within plant communities, by combining a community ecology approach with germination ecology. Further research is needed to clarify e.g. the role of clonality in compensating the lack of germination of foredune foundation species due to climate change, and to investigate general patterns such as the "azonal" germination strategy of seaward-located species. However, our results suggest that coexisting species differentiate their niche in their very early phase

of the life cycle, i.e. the seed germination niche, thereby having different opportunities of seedling establishment.

By considering not only the species composition, but also their relative functional roles, we related the germination niche to the foredune community assembly and dynamics to help disentangling possible local from broader effects of environmental changes on coastal systems. Results can be used to forecast foredune community responses to changing environmental conditions and as a valuable tool for restoring healthy ecosystems and the supporting services and benefits they provide.

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Table 1 Phi coefficient and frequency values for the 19 species found in the foredune group of plots. Foundation species of the foredune system are highlighted in bold. Alien species are marked with (*). Accidental species which came from the semi-fixed dune are marked with ('). For each species also the life cycle, the growth form, and the month in which seeds were collected are reported. <u>Growth form</u>: Erect leafy: plants with leaves concentrated in middle and/or top parts; Semi-basal: significant leaf area deployed both close to the soil surface and higher up the plant; Short basal: leaves concentrated very close to the soil surface (e.g. rosette plants or prostrate growth forms); Tussocks: many leaves from basal meristem forming prominent tufts. <u>Reproductive strategy</u>: S, by seed; SSV, mostly by seed, rarely vegetative; SV, by seed and vegetative; VVS mostly vegetative, rarely by seed. The reproductive strategies marked with "[1]" were assigned based on field observations, because information was not available from BiolFlor database.

	Species	Synonym		Foredune		Semi-fixed dune		Fixed dune	Life cycle	Growth form	Reproductive strategy	Seed collecting (month)
			Phi	Frequency (%)	Phi	Frequency (%)	Phi	Frequency (%)				
	Numbers of plots			60		403		41				
1	*Calamagrostis arenaria*	*Ammophila arenaria* (L.) Link	83	85	---	7	---	0	Perennial	Tussock	VVS	July
2	*Cakile maritima*		49.6	37	---	2	---	0	Annual	Erect leafy	S	August

	Species	Synonym							Life history	Growth form		Month
3	*Thinopyrum junceum*	*Elymus farctus* (Viv.) **Runemark ex Melderis**	**46.9**	**42**	---	9	---	0	Perennial	Tussock	SV	August
4	*Salsola kali*		**42.3**	**25**	---	1	---	0	Annual	Erect leafy	S	August
5	*Calystegia soldanella*		---	**23**	---	12	---	5	Perennial	Short basal (prostrate)	SV	July
6	*Echinophora spinosa*		---	**8**	---	7	---	0	Perennial	Erect leafy	SSV[1]	October
7	*Euphorbia peplis*	*Chamaesyce peplis* (L.) **Prokh.**	---	**5**	---	0	---	0	Annual	Short basal (prostrate)	S[1]	August
8	*Eryngium maritimum*		---	**5**	---	4	---	0	Perennial	Erect	S	August

		leafy								
9	*Euphorbia paralias*		---	**3**	---	1	---	0	Perennial	Erect leafy	S[1]	August
10	*Festuca fasciculata* [ᵗ]	*Vulpia fasciculata* (Forssk.) Fritsch	---	5	70.2	68	---	2	Annual	Tussock	S[1]	May
11	*Cyperus capitatus* [ᵗ]	*Cyperus kalli* (Forssk.) Murb.	---	2	53.2	40	---	0	Perennial	Short basal (rosette)	VVS[1]	June
12	*Medicago littoralis* [ᵗ]		---	7	26.5	22	---	2	Annual	Short basal (prostrate)	S[1]	May
13	*Hypochaeris radicata* [ᵗ]		---	5	19.3	19	---	7	Perennial	Short basal (rosette)	SSV	June

14	*Silene colorata* (¹)	*Silene canescens* Ten.	---	2	---	9	---	0	Annual	Erect leafy	S[1]	May
15	*Xanthium strumarium* subsp. *strumarium* (*)	*Xanthium orientale* L.	91.2	93	---	5	---	0	Annual	Erect leafy	S[1]	August
16	*Cenchrus longispinus* (*)		30.2	27	---	11	---	0	Annual	Semi-basal	S[1]	September
17	*Oenothera stucchii* (*)	*Oenothera biennis* L. group	---	15	48.5	52	---	2	Biennial	Semi-basal	S	September
18	*Ambrosia psilostachya* (*)	*Ambrosia coronopifolia* Torr. & A.Gray	---	38	29.7	70	---	39	Perennial	Semi-basal	VVS	September
19	*Erigeron canadensis* (*)	*Conyza canadensis* (L.) Cronquist	---	18	---	19	---	0	Annual	Erect leafy	S	August

Table 2 Mean values (± sd) of seed mass and shape index of the dispersal unit. Values with different letters are significantly different to post hoc Tukey test.

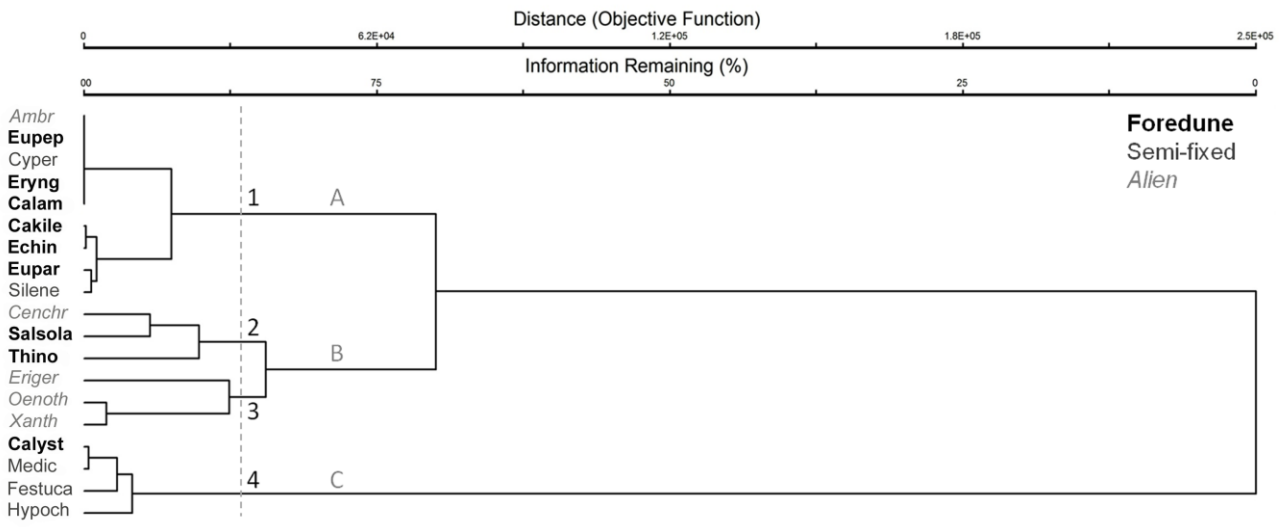| Cluster	Seed mass (mg)			Shape Index (dispersal unit)		
	Mean	± sd		Mean	± sd	
Low- germinating	7.32	6.80	A	0.13	0.08	a
Dark warm-cued	5.85	2.25	A	0.12	0.10	a
Light warm-cued	3.23	2.90	A	0.05	0.04	b
High-germinating	9.80	17.53	A	0.15	0.12	a

FIGURE CAPTIONS

Fig 1 Cluster dendrogram performed on the matrix of 19 species x 10 variables (germination at 5 temperatures x 2 photoperiods). Species abbreviations: *Ambrosia psilostachya* (Ambr); *Calamagrostis arenaria* (Calam); *Cakile maritima* (Cakile); *Calystegia soldanella* (Calyst); *Cenchrus longispinus* (Cenchr); *Cyperus capitatus* (Cyper); *Echinophora spinosa* (Echin); *Erigeron canadensis* (Eriger); *Eryngium maritimum* (Eryng); *Euphorbia paralias* (Eupar); *Euphorbia peplis* (Eupep); *Festuca fasciculata* (Festuca); *Hypochaeris radicata* (Hypoch); *Medicago littoralis* (Medic); *Oenothera stucchii* (Oenoth); *Salsola kali* (Salsola); *Silene colorata* (Silene); *Thinopyrum junceum* (Thino); *Xanthium strumarium* subsp. *strumarium* (Xanth). Foundation species of the foredune system are highlighted in bold.
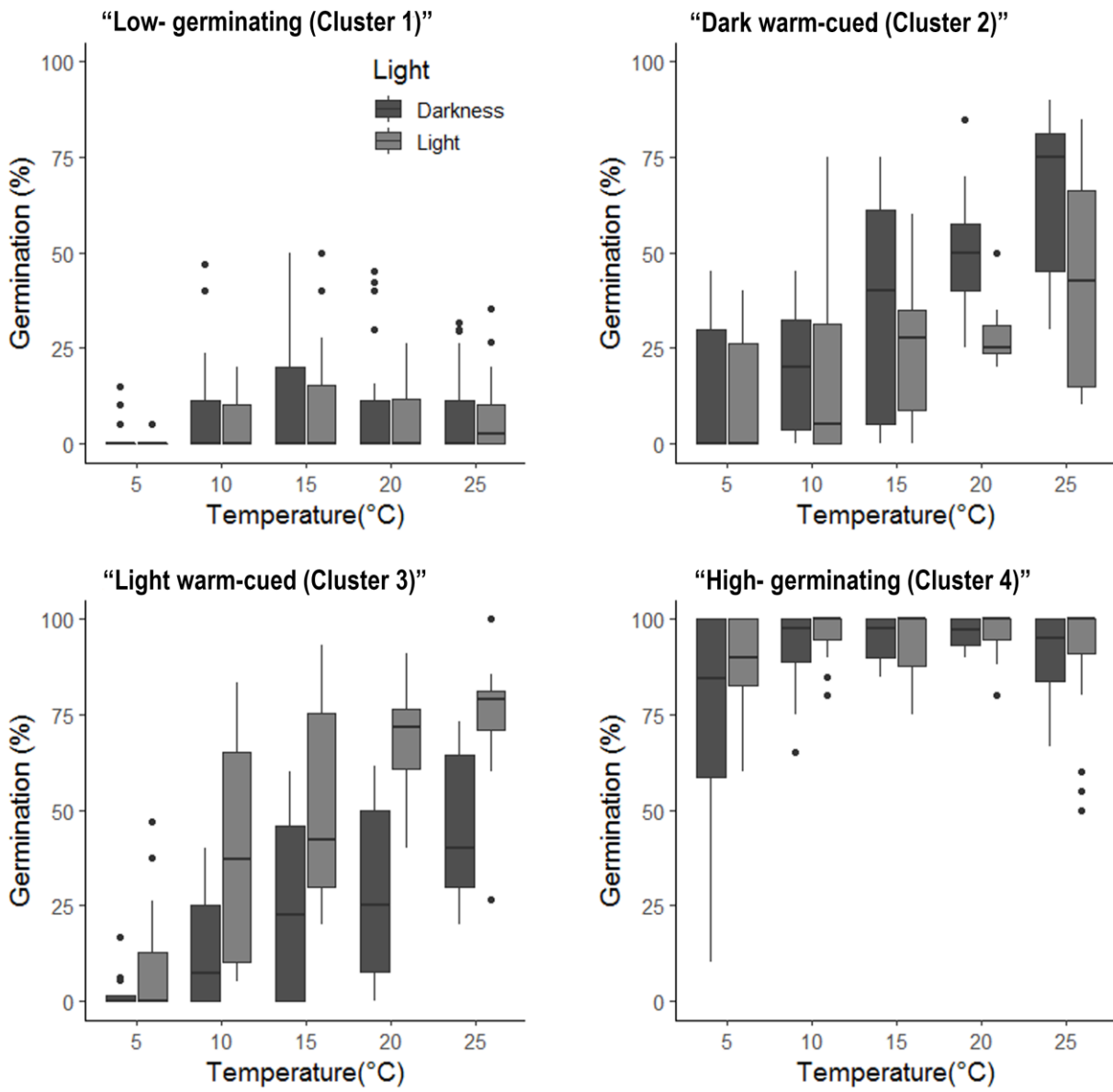
Fig 2 Box plots representing the germination percentage for each Cluster evidenced by cluster analysis. Dark grey boxes indicate germination in 24h darkness, while light grey boxes indicate germination at 12/12h photoperiod.

Figure 1

Figure 2