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The germination niche of coastal dune species as related to their occurrence along a sea–inland gradient

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Abstract

Aims: The early phases in the life cycle of a plant are the bottleneck for successful species establishment thereby affecting population dynamics and distribution. In coastal environments, the spatial pattern of plant communities (i.e. vegetation zonation) follows the ecological gradient of abiotic stress changing with the distance from the sea. This pattern has been mainly explained based on the adaptation and tolerance to the abiotic stress of adult plants. However, the adult niche may considerably differ from the germination niche of a plant species. The aim of this work was to investigate to what extent abiotic factors (specifically salinity, temperature, nitrogen and their interactions) constrain seed germination along the sea–inland gradient.

Location: Latium coast (Central Italy).

Methods: Germination tests were performed on seeds of focal species of three different plant communities which establish at increasing distances from the coastline: *Cakile maritima* subsp. *maritima*, *Elymus farctus*, *Crucianella maritima*. We tested increasing concentrations of NaCl (one of the main abiotic factors which decrease across the sea–inland gradient), and their interactions with temperature and KNO₃, to consider other factors which drive germination processes.

Results: The tolerance to salinity significantly decreased in relation to the position of species along the coastal zonation. *Crucianella maritima* was shown to be the least tolerant species, having a decrease in germination >80% across all conditions. KNO₃ significantly (although slightly) increased the germination percentage in *Cakile maritima* subsp. *maritima* and *Elymus farctus*. When combined with NaCl, KNO₃ alleviated the negative effects of salinity only in *Cakile maritima* subsp. *maritima*. **Conclusions:** The germination responses to the interaction among the tested factors suggest that the germination niche may explain vegetation zonation filtering species at their early stages. Quantifying environmental niches in different phases of the life cycle of plants may provide important insights into community assembly processes.

KEYWORDS

adaptation, environmental gradient, germination, Mediterranean basin, nitrogen, psammophilous vegetation, salinity, temperature

1 INTRODUCTION

Post-dispersal processes as germination and seedling development are the bottleneck for successful species establishment, and thus are key determinants of species distribution patterns and population dynamics (Grubb, 1977; Donohue *et al.*, 2010; Huang *et al.*, 2010; Poschlod *et al.*, 2013; Cogoni *et al.*, 2019). At the same time, such early stages of the plant's life cycle are strongly affected by environmental factors and are recognised as the most vulnerable phases for plant establishment (Walck *et al.*, 2011; Parmesan & Hanley, 2015; Slaviero *et al.*, 2016). However, patterns of species coexistence or spatial distribution in relation to environmental factors have been mainly explained taking into consideration adult plants, while other stages have often been overlooked, despite their important role in plant establishment (Fantinato *et al.*, 2018). Specifically, the regeneration niche (Grubb, 1977; Poorter, 2007), i.e. the set of environmental requirements necessary for germination and establishment of a plant species, may differ from the adult niche, and the analysis of the responses of early phases to varying environmental conditions may significantly contribute to elucidating ecological processes related to vegetation dynamics (Jiménez-Alfaro, *et al.*, 2016; Saatkamp *et al.*, 2019).

In coastal dunes, factors such as salinity, soil temperature and moisture, nutrient availability, wind intensity, and sand burial change sharply from the coastline inland, leading to the formation of vegetation belts arranged parallel to the coastline, which can be identified by the species turnover (i.e. "vegetation zonation"; Doing, 1985; Torca *et al.*, 2019). The drift line, which is exposed to marine influence more than the other zones, is characterised by intense wind and salt spray (Martínez & Psuty, 2004; Fenu *et al.*, 2013; McLachlan & Defeo, 2017). As a consequence of sparse vegetation cover, the soil is exposed to intense solar radiation, and can reach high temperature values (up to 60°C at the surface; Martínez & Psuty, 2004; Maun, 2009). The marine influence, e.g. wind intensity and salinity, gradually decreases inland, and makes semi-fixed and fixed dunes less limiting for species survival. Soil temperature is often lower on the dunes than in the drift line, because of the shade provided by the higher vegetation cover (about 10°C lower than in bare soil; Martínez & Psuty, 2004; Rajaniemi & Barrett, 2018). Nutrients, which are mostly represented by nitrates, are generally scarce, except for the drift line and the fixed dune, where they are more abundant than in the shifting dunes (Martínez & Psuty, 2004; McLachlan & Defeo, 2017). This environmental gradient is the main driver of the species turnover from the sea to inland, leading to the formation of vegetation belts arranged parallel to the coastline (i.e. "vegetation zonation"; Doing, 1985; Torca *et al.*, 2019).

The vegetation zonation represents a striking peculiarity of coastal environments worldwide, and features such as the number of belts, their connectivity, spatial extent, and species composition are regarded as useful indicators of the conservation status of coastal systems, since their modification indicates possible alteration of the system functionality (Buffa *et al.*, 2005; Carboni *et al.*, 2009; Gigante *et al.*, 2016; Fenu *et al.*, 2017; Pinna *et al.*, 2019; Del

Vecchio *et al.*, 2018). The turnover of species along the sea-inland gradient has been traditionally explained by adaptations and tolerance of adult plants to abiotic factors (Fenu *et al.*, 2013; Bazzichetto *et al.*, 2016; Torca *et al.*, 2019). In fact, research showed that environmental factors such as salinity and soil temperature select the most tolerant species to establish closer to the sea (e.g. *Cakile maritima*, *Salsola kali*), while the species less adapted to withstand abiotic stress are constrained to grow in the inner, more protected, zones (e.g. dwarf shrubs of semi-fixed dunes; Silan *et al.*, 2017; Del Vecchio *et al.*, 2018; Fantinato *et al.*, 2018).

However, there may be no match between adults and the germination phase in terms of their tolerance to abiotic factors. For example, while adult plants may tolerate high salt concentration as well as high temperature, in some cases they proved to be very salt-sensitive during the germination phase and seedling development (Gul *et al.*, 2013; Yuan *et al.*, 2019), especially at high temperature (El-Keblawy & Al-Shamsi, 2008; Manzoor *et al.*, 2017; Santo *et al.*, 2017). Although the treatment effects vary across species, literature demonstrated that NaCl concentrations higher than 250 mM can completely suppress germination (Del Vecchio *et al.*, 2012; Delgado Fernández *et al.*, 2016; Santo *et al.*, 2017; Del Vecchio, Porceddu *et al.*, 2019), while long exposure time can have detrimental effects, leading to seed mortality (Saeed *et al.*, 2011; Santo *et al.*, 2014; Del Vecchio, Porceddu *et al.*, 2018).

Temperature is a regulator of germination timing, and its role is particularly important in systems with a marked seasonality, such as those of the Mediterranean or Temperate regions, where temperature fluctuations within the year might be stronger than among different years (Baskin & Baskin, 2014). During the transition from seed to seedling, species are often quite sensitive to extreme temperatures and thermal cues regulate germination to occur during the best period for seedling survival (Baskin & Baskin, 2014). However, adult species may tolerate a different temperature range, using morphological and physiological adaptations to withstand freezing or overheating (Larcher, 2003).

Similarly to salinity and temperature, other factors such as nutrient availability, which also vary along the sea-inland gradient, are known to significantly influence the germination process (Hilhorst & Karssen, 2000) and may contribute to the vegetation zonation selecting species based on their requirements during germination. It has been shown that K and N compounds can affect germination (Atia *et al.*, 2009; Duermeyer *et al.*, 2018). KNO₃ has been recognised as a germination promoter (Pons, 1989), increasing both seed germination percentage and germination speed in several species (Duermeyer *et al.*, 2018). Effects on germination can also derive from the interaction of KNO₃ and NaCl, although with contrasting patterns. Specifically, KNO₃ has been proven to alleviate salt-induced stress in several species (Neid & Biesboer, 2005; Atia *et al.*, 2009; Zehra *et al.*, 2013) including *Elymus farctus* (El-Katony *et al.*, 2015). Conversely, KNO₃ could not alleviate the effect of salinity in *Silene mollissima* aggregate (Murru *et al.*, 2015) and in *Vicia faba* (Abd El-Baki *et al.*, 2018). However, unlike salinity and temperature, which in general decrease linearly from the sea

inland, nutrient levels have a more complex distribution pattern with an uneven, bimodal trend, being at higher concentrations in the fixed dune and along the drift line, mainly due to higher litter deposition, and decomposition of seagrass wrack deposits, respectively (McLachlan & Defeo, 2017).

Temperature, salinity and nitrogen have often been investigated in seed ecology research (e.g. Gul *et al.*, 2013; Baskin & Baskin, 2014; Duermeyer *et al.*, 2018); however, only seldom research considered their interactions in relation to coastal zonation. In this context, the aim of this work was to investigate whether there is a relationship between seed germination responses to abiotic factors and the adult spatial distribution pattern along the coastal gradient. To this end, we selected three species typical of different belts of the coastal zonation (*Cakile maritima* subsp. *maritima*, *Elymus farctus*, *Crucianella maritima*) and set out an experiment to analyse their germination niche with respect to salinity, also considering its interactions with temperature and nitrogen. We hypothesise that, irrespective of the adult niche, germination requirements have a role in shaping vegetation patterns and the distribution of species along the coastal environmental gradient by selecting halo-nitrophilous species near the coastline (*Cakile maritima* subsp. *maritima*), salt-tolerant species beyond the first belt of vegetation (*Elymus farctus*), and salt-sensitive species more inland (*Crucianella maritima*).

2 | METHODS

2.1 Study site

Seeds of the three species were collected in Central Italy, along the Latium coast (between Torre Flavia, latitude and longitude, DD: 41.96171366, 12.04590248, and Passoscuro, 41.912327, 12.145901). The area is characterised by a Mediterranean Pluviseasonal Oceanic (MPO) bioclimate, with hot and dry summer and mild rainy winter (Rivas-Martínez *et al.*, 2004). The changes in salinity, soil temperature, nutrients, wind intensity and sand burial, and the position of the target species along the vegetation zonation are represented in Figure 1.

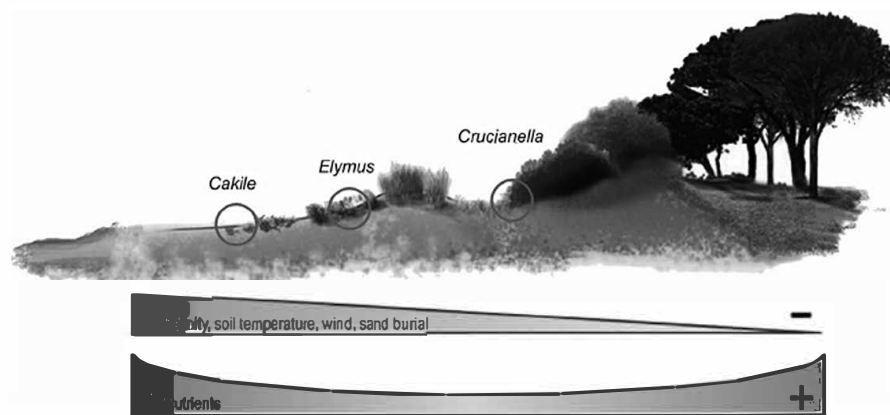


FIGURE 1 Scheme of the vegetation zonation in relation to the main environmental factors along the sea-inland gradient. The target species of this work, *Cakile maritima* subsp. *maritima*, *Elymus farctus*, and *Crucianella maritima*, occupy different belts, at increasing distances of the coastline (modified from Acosta and Ercole 2015)

2.2 Seed collection

We selected focal species (namely the key species pivotal to habitat structure and function; e.g. Benson, 2006; Lindgaard & Henriksen, 2011; Keith *et al.*, 2013) of three different plant communities that thrive at increasing distance from the coastline, subjected to progressively less harsh environmental condition: (i) *Cakile maritima* subsp. *maritima* (hereafter referred to as *Cakile*), an annual species of the drift line, i.e. the vegetation zone closest to the coastline; (ii) *Elymus farctus* (hereafter referred to as *Elymus*), a perennial herbaceous of the embryonic shifting dunes; (iii) *Crucianella maritima* (hereafter referred to as *Crucianella*), a dwarf shrub of Mediterranean semi-fixed dunes (Acosta *et al.*, 2003). Species nomenclature follows Bartolucci *et al.* (2018).

Seeds were collected from 80 randomly selected individuals, at the time of natural dispersal (in mid-July 2017 for all the species) and sent to the Sardinian Germplasm Bank (BG-SAR) of the University of Cagliari (Italy), where they were manually cleaned. To enable equal conditions among seeds, they were after-ripened at room temperature (20°C and 40% relative humidity [RH]) for 40 days, dehydrated (15°C and 15% RH) and stored at 5°C until the experiment started, for a total of 90 days.

2.3 Germination tests

Four replicates of 20 seeds each were used for each test. Seed was sown in Petri dishes on 1% water agar, and incubated in growth chambers (Sanyo MLR-351, Sanyo Electric Co., Ltd, Wakehurst Place, UK). We selected a range of temperature that, according to the literature (Debez *et al.*, 2004; Del Vecchio *et al.*, 2012; El-Katony *et al.*, 2015), allowed a good germination percentage (higher than 50%) for the target species and that was representative of the seasons of the study area. Monthly temperature values, averaged for the period 2004–2017, were retrieved from <http://www.arpalazio.gov.it/>. Therefore, seeds were exposed to 20°C, which corresponded to the average temperature in late spring (May–June) and early autumn (September–October), and to 25°C, which corresponded to the average temperature in summer (July–August; Del Vecchio, Porceddu

et al., 2019). Following previous studies, *Cakile* and *Crucianella* were incubated in darkness (Debez et al., 2004; Del Vecchio et al., 2012), achieved by wrapping the dishes in two layers of aluminium foil, while *Elymus* was incubated in a 12/12 light/dark photoperiod (Royal Botanic Gardens Kew, 2008).

To test the effect of salinity, nitrogen and their interaction, seeds were incubated at the same temperature and light regimes on 1% water agar, with different solutions. To test the effects of different salt concentrations, we used NaCl at 125 and 250 mM. These concentrations were selected on the basis of a geometric series spaced by a factor of 0.5 (OECD, 2006). We started from NaCl seawater concentration (500 mM) and considered as testing conditions its dilution at 50% (250 mM) and 25% (125 mM). We excluded to test NaCl 500 mM because it has already been demonstrated that it suppressed the germination for the target species (Debez et al., 2004; Del Vecchio et al., 2012; El-Katony et al., 2015). We also excluded NaCl concentrations that represented seawater dilution beyond 25% (12.5%, corresponding to a NaCl concentration of 62.5 mM) because for several species germination was not different from that in freshwater, while differences have been observed at NaCl higher than 100 mM (including *Cakile maritima* and *Elymus farctus*; Debez et al., 2004; Guja et al., 2010; El-Katony et al., 2015). To test the effect of nitrogen, we used KNO₃ (10 mM) as nitrogen source. Despite both nitrates and ammonium being present in the field (Martínez & Psuty, 2004; Maun, 2009), nitrates are often more abundant than ammonium (Alpert & Mooney, 1996;

Kachi & Hirose, 1983; Bonanomi et al., 2012), especially at the alkaline pH observed in coastal dunes along the Tyrrhenian coast (Kooijman & Basse, 2002; Fenu et al., 2012; Ruocco et al., 2014; USDA, 2014). The selected concentration falls within the range of possible substrate nitrogen contents measured in the field (Pizzo, 2012). Moreover, KNO₃ at the concentration of 10 mM was widely used, and proved to have positive effects on seed germination, and in alleviating salinity stress (Atia et al., 2009; Duermeyer et al., 2018). To test the interaction of salinity and nitrogen we used a mixed solution with NaCl 125 mM and KNO₃ 10 mM. We used only the lowest concentration of NaCl because from preliminary tests it proved to significantly reduce or suppress the germination of the target species.

For all the tests, seeds were scored only once, at the end of the experiment after 75 days from sowing. At the end of the test, non-germinated seeds were cut (Ooi et al., 2004; FAO, 2014), observed under the stereoscope and classified as viable, died or empty, and the final number of germinated seeds was calculated based on the total number of filled seeds.

2.4 Data analyses

Germination of the three species at different temperatures was compared by two-way PERMANOVA with 9,999 randomisations (Past software; Hammer et al., 2001; Anderson, 2014) followed by a

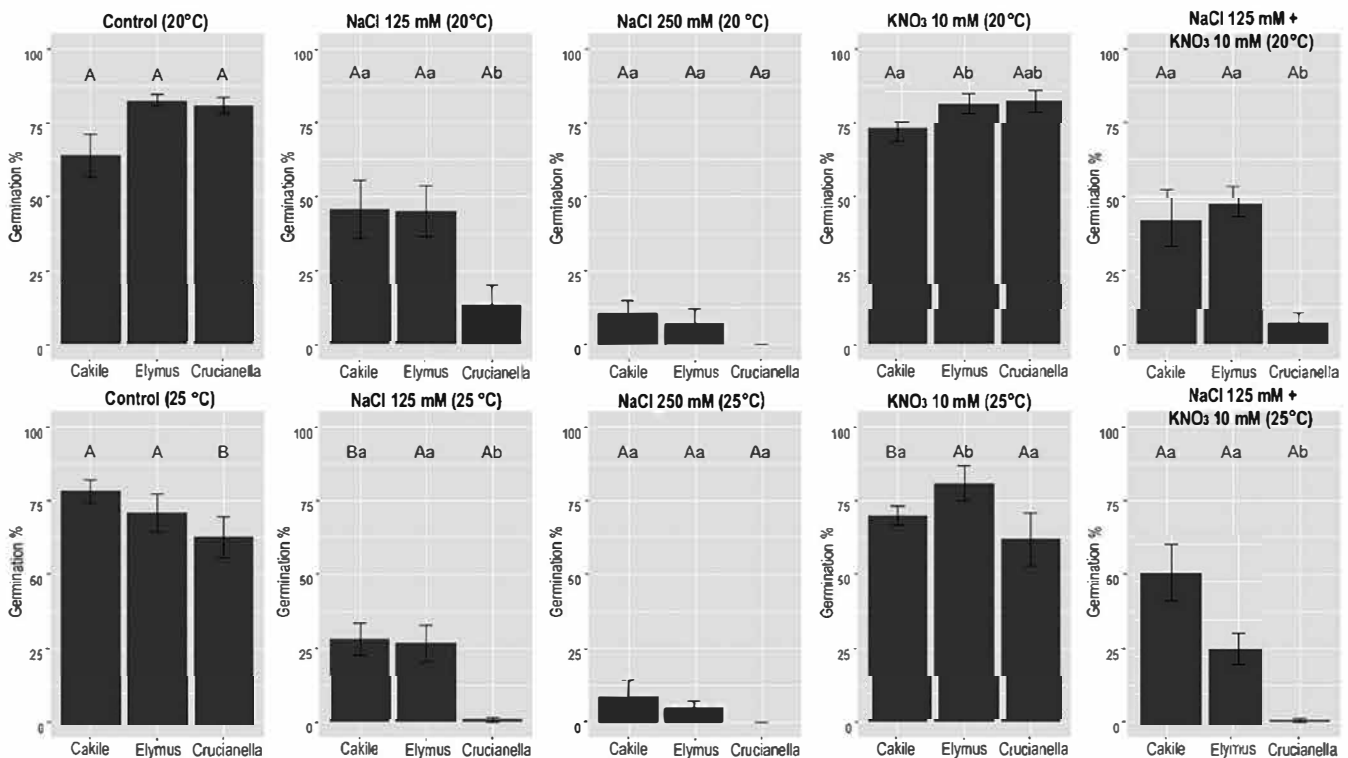


FIGURE 2 Germination percentage (mean \pm SE) for each species, at each condition. Bars with different letters are significantly different in a post-hoc Fisher test. Lowercase letters indicate differences across species, at the same condition. Capital letters indicate differences within species across temperature. Significant differences between the decrease in germination at NaCl 125 mM and the combined solution of NaCl and KNO₃ are indicated only in the text

TABLE 1 Variation in germination percentage (mean \pm SD) for each species at each condition compared to control (PERMANOVA and post-hoc Fisher test). Negative values indicate decrease, while positive values indicate increase in germination percentage compared to seed sown in agar only, at 20°C and 25°C

| Temperature (°C) | NaCl 125 mM | | | NaCl 250 mM | | | KNO ₃ 10 mM | | | NaCl 125 mM + KNO ₃ 10 mM | | |
|--------------------|-------------|------------|--|-------------|------------|--|------------------------|------------|--|--------------------------------------|------------|--|
| | Mean | SD | | Mean | SD | | Mean | SD | | Mean | SD | |
| 20 | | | | | | | | | | | | |
| <i>Cakile</i> | -36.3 | \pm 33.5 | | -85.4 | \pm 17.2 | | 33.3 | \pm 78.8 | | -30.8 | \pm 33.2 | |
| <i>Elymus</i> | -44.5 | \pm 27.1 | | -90.3 | \pm 15.3 | | 1.4 | \pm 12.2 | | -40.2 | \pm 13.2 | |
| <i>Crucianella</i> | -84.6 | \pm 18.7 | | -100.0 | \pm 0.0 | | 7.1 | \pm 18.3 | | -88.1 | \pm 9.9 | |
| 25 | | | | | | | | | | | | |
| Temperature (°C) | Mean | SD | | Mean | SD | | Mean | SD | | Mean | SD | |
| <i>Cakile</i> | -64.3 | \pm 21.3 | | -89.1 | \pm 19.4 | | -8.4 | \pm 18.5 | | -33.1 | \pm 28.1 | |
| <i>Elymus</i> | -61.6 | \pm 21.6 | | -92.2 | \pm 9.4 | | 21.3 | \pm 44.9 | | -57.1 | \pm 28.3 | |
| <i>Crucianella</i> | -99.0 | \pm 2.4 | | -100.0 | \pm 0.0 | | -9.8 | \pm 31.7 | | -98.5 | \pm 3.7 | |

post-hoc Fisher test, using germination percentage as response variable, and temperature and species as grouping variables.

To compare germination responses to salinity, nitrogen, the combined solution, and their interaction with temperature among the species, we focused on the variation in germination with respect to germination in agar only (control). At each temperature, we calculated the percentage of increase or decrease in germination under NaCl, KNO₃, and their combination, with respect to the control. This allowed measuring the intensity of the response of the species to the same factors, independently of their absolute germination values. We assumed that species that show intense variation to a factor are more sensitive than species that show a low variation.

To analyse if the variation in germination differed among species, we used one-way PERMANOVA, with 9,999 randomisations. As grouping variable, we used species at each condition of temperature and tested solution. Differences among species at the same condition and within species over temperature were assessed by a post-hoc Fisher test.

3 RESULTS

All the species had a germination percentage higher than 50% at all tested temperatures (Figure 2, "Control" bar plots). Germination percentages averaged by temperature were $70.9 \pm 17.8\%$ for *Cakile*, $76.7 \pm 12.9\%$ for *Elymus*, and $71.7 \pm 15.7\%$ for *Crucianella*. However, species differed in their response to changes in temperature (two-way PERMANOVA test; $p < 0.001$). Specifically, *Cakile* and *Crucianella* showed opposite trends: *Cakile* had a higher germination percentage at high temperature, although the increase was not significant ($63.8 \pm 20.8\%$ at 20°C vs $78.1 \pm 11.3\%$ at 25°C; post-hoc Fisher test, $p = 0.05$), while *Crucianella* showed higher values at moderate temperature ($80.8 \pm 6.6\%$ at 20°C vs $62.5 \pm 17.2\%$

at 25°C; post-hoc Fisher test, $p = 0.03$). *Elymus* showed a lower germination percentage at 25°C, but the difference was not significant ($82.5 \pm 5.2\%$ at 20°C vs $70.8 \pm 15.9\%$ at 25°C; post-hoc Fisher test, $p = 0.17$).

Regarding salinity and nitrogen, one-way PERMANOVA revealed significant differences among species at the same condition and within species between temperatures ($F = 15.01$; $p = 0.0001$). Overall, salinity had a detrimental effect on the germination percentage and at NaCl 250 mM: germination was suppressed for all the species, producing a decrease in the range of 85%–100% at each temperature (Table 1; Figure 2).

At NaCl 125 mM, *Cakile* appeared to be the most salt-tolerant species, showing a decrease in germination of about 35–65% across temperature (Table 1; Figure 2). *Elymus* showed a decrease in germination comparable to *Cakile*, although a little higher (in the range of 45–65%). In both species, increasing temperature exacerbated the negative effect of salinity, although the difference was significant only for *Cakile*. *Crucianella* exhibited the lowest tolerance to salinity, consistently showing a decrease in germination higher than 80% at all tested temperatures.

Germination had a narrow range of variation under KNO₃. It showed a fluctuating pattern, increasing or decreasing on average by less than 10% compared to germination in the control. The highest effects were an increased germination in *Cakile* at 20°C, which was 33% higher compared to control, and in *Elymus* at 25°C (about 20% higher than control; Table 1; Figure 2).

The combined solution of NaCl and KNO₃ had a slight effect on the germination percentage, with the only significant positive effect being observed in *Cakile* at its optimal germination temperature (post-hoc Fisher test; $p = 0.01$ between decrease in germination under NaCl 125 mM and the combined solution, at 25°C). In *Elymus* and *Crucianella*, KNO₃ did not significantly alleviate the effect of salinity at any of the tested temperatures.

4 DISCUSSION

Our results showed that the focal species, which are typical of successive vegetation belts of Mediterranean sandy coastal systems, have different germination responses to temperature, salinity, nitrogen and their interaction. Although the distribution of species in the field results from the combination of several factors (e.g. abiotic and biotic interactions), our results suggest that the germination niche of the focal species may contribute to determine their distribution in coastal dunes, precluding salt and high temperature-sensitive species to germinate near the coastline.

4.1 Effect of temperature

Although we tested a narrow range of temperatures, it was possible to observe a different response in the target species, with a decreasing tolerance according to their typical position along the sea–inland gradient. *Cakile*, a characteristic species of the drift line, showed adaptation to high temperature, with decreasing germination percentage at the lowest tested value. *Elymus*, characteristic of the embryo dune, exhibited a wider niche, being able to germinate at both temperatures at comparable percentages. Conversely, *Crucianella*, narrowly restricted to semi-fixed dune grasslands, most successfully germinated at the lower temperature tested. These results are in line with those of Rajaniemi and Barrett (2018), who found a similar trend, with species able to germinate at high temperature mostly located near to the coastline, and species with lower tolerance establishing in the inner zones. Although our results are based on laboratory tests, and on three species representative of different vegetation belts, they suggest that an optimal temperature requirement for a maximum germination percentage could be considered in this way as an adaptive strategy (Hesp, 1991). However, previous studies which analysed coastal dune species during the adult phase reported that species of coastal grasslands of semi-fixed dunes are more thermophilic (i.e. adapted to tolerate high temperature during the adult phase) than the species of the drift line and fixed dune (Isermann, 2011; Del Vecchio *et al.*, 2015). Therefore, we could suggest that compared to the adult phase, for the tested species the response to temperature along the sea–inland gradient has opposite trends during the germination. A higher number of species should be analysed for a more comprehensive understanding of high temperature tolerance and the possible difference between the germination and the adult phase.

Temperature has most often been used to explain temporal patterns of germination, since the highest variations occur in relation to seasons (Martínez & Psuty, 2004; Baskin & Baskin, 2014; Santo *et al.*, 2019). In fact, the ability of *Cakile* and *Elymus* to germinate at high temperature may be related to their adaptation to emerge in late spring and summer, while *Crucianella*, which is adapted to moderate temperatures, is more likely to emerge in early spring and autumn (Davy *et al.*, 2006; Del Vecchio *et al.*, 2012; Baskin & Baskin, 2014). In addition, such a seasonal pattern could also be related to the spatial

distribution of species along the sea–inland gradient. Indeed, germination at higher temperatures, which in Mediterranean temperate climates coincide with the summer season, prevents the species growing close to the coastline to emerge in winter, which represents the most limiting period for the strandline, due to intense storms and excessive sand burial (Fernández-Pascual *et al.*, 2017). On the contrary, germination in early spring and autumn, usually observed in inland species, prevents seedling to emerge in summer, which represents the most critical season due to water stress (Fernández-Pascual *et al.*, 2017). Comparison of the Mediterranean systems with others, such as tropical systems or those of cold temperate regions, will be useful to explore whether and which patterns can be generalised, and which ones are more dependent on local adaptation.

4.2 Effect of salinity

Our study showed that substrate salinity acts as a major selective force in seed germination for the target species. At NaCl 250 mM, germination was hindered at all tested temperatures, also in *Cakile*, which is commonly described as tolerant of salt spray and transient inundation by seawater (Davy *et al.*, 2006), allowing this concentration to be defined as a threshold for germination. However, the detrimental effects of salinity were also apparent at lower concentrations, with a linearly decreasing trend in the germination percentage from *Cakile* to *Crucianella*, and the negative effect of salinity was higher at higher temperature.

Despite its linear and often marked decreasing gradient from the sea inlands, soil salinity has been assumed to play a secondary role in explaining the spatial distribution of adult plants if compared to other factors such as soil nutrient content, sand grain size, or water availability (Isermann, 2011; Fenu *et al.*, 2013; van Puijenbroek *et al.*, 2017). According to Maun (2009), shoreline plant species are largely unaffected by the natural levels of salt deposition. In fact, adult plants are able to withstand salt, and the selection pressure for tolerance to substrate salinity is weak (Maun, 2009; Gul *et al.*, 2013). Therefore, given the disruptive role of salinity in the germination phase observed in our study, we suggest that in coastal species salinity is the bottleneck for successful germination and seedling establishment, contributing in this way to the species distribution patterns by acting during early stages. Near the coastline, substrate salinity should filter out those species that are not able to germinate under saline conditions, especially if coupled with high temperature.

4.3 Effect of nitrogen

Although it was not possible to identify a clear trend, we observed weak responses to nitrogen for all tested species. Only *Cakile* and *Elymus* showed a slight significant increase in germination, suggesting that they may benefit from the nutrients mainly derived from decomposing wrack on the strandline. Moreover, our results demonstrate that the interaction of nutrients with temperature plays

a more important role, compared to nutrients alone. The capacity of nutrients to improve germination as well as their capacity to alleviate salt stress becomes significant only at a species-specific temperatures.

However, previous studies showed that nutrient availability significantly enhances seedling growth rate, improving their establishment (Maun, 1994; Del Vecchio *et al.*, 2013) by incrementing seedling biomass (Frosini *et al.*, 2012), and counteracting the effect of sand burial (Gilbert *et al.*, 2008). Similarly to nitrogen alone, the interaction of nitrogen and salinity also seems to be particularly important during the post-germination phase: nitrogen supply proved to alleviate the toxic effect of salinity in seedlings, enhancing the activity of antioxidant enzymes in several species (Zheng *et al.*, 2008; Abd El-Baki *et al.*, 2018; Ibrahim *et al.*, 2018). Therefore, we could affirm that nutrients such as nitrogen could limit species survival in adults but seems to have a less important role in the germination of coastal species.

5 | CONCLUSIONS

Our study explored the germination responses of typical coastal dune species to temperature, salinity, nitrogen and their interactions. Our results not only confirmed trends already known for plants of different zones but also for the first time directly compared the role of salinity and nutrients, and their interaction with temperature to explain the distribution of the study species in coastal dunes. Overall, our results suggest that the germination niche contributes to determine species distribution and turnover in coastal dunes, precluding salt- and high temperature-sensitive species to germinate near the coastline. Besides this, our research highlighted the importance of considering the interaction among factors during the germination phase. Consistent with previous research, we suggest that in coastal species salinity is the bottleneck for successful establishment; however, its negative effect can be either alleviated or exacerbated depending on the interactions with temperature and nitrogen. Moreover, our study suggests that the environmental niche in coastal dune species can vary across their life cycle, confirming the pivotal importance of gathering information on each stage of a species' life cycle. Broadening our point of view can effectively contribute to elucidate species dynamics, species' spatial distribution and patterns of species assembly.

Although germination strategies revealed by laboratory tests should be compared with caution with germination in the field, our research represents a useful approach to including the germination niche in ecological studies and lays the foundation for disentangling the role of early stages of a plant's life cycle in the population dynamics and species distribution patterns.

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AUTHOR CONTRIBUTIONS

SDV, GB, AA, and GB conceived the research idea; SDV collected data; SDV, with contributions from all authors, wrote the paper.

DATA AVAILABILITY STATEMENT

The datasets generated during the current study are available from the corresponding author on reasonable request.

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