Initial constraints in seedling dynamics of *Juniperus macrocarpa* Sm.

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Abstract The micro-forests dominated by *Juniperus macrocarpa* inhabiting coastal dunes in the Mediterranean Basin are European priority habitats. Their conservation is hindered by both anthropic and natural causes, although the regeneration problems for *J. macrocarpa* are still poorly understood. In this study, several factors influencing emergence and mortality of *J. macrocarpa* seedlings were investigated. For this purpose, permanent plots were placed in coastal dunes of Sardinia (Italy) and periodically monitored to record seedling parameters (emergence, survival and growth), as well as several biotic and abiotic variables (solar radiation, tree cover, herbaceous plus scrub cover, number of female cones on the soil and number of herbivory traces). Linear mixed models were fitted to test the effects of several types of explanatory variables on seedling dynamics. A total of 536 seedlings were marked, most of which emerged in winter. The microhabitat was the most important factor in models explaining emergence, with the number of emerged seedlings decreasing with solar radiation. Survival was very low, reaching the highest mortality percentage in the first summer. Herbivory and location in open interspaces had significant negative effects on seedling survival. In conclusion, the recruitment of *J. macrocarpa* is highly limited in the initial life cycle phases, with microhabitat and herbivory constraints influencing seedling dynamics. The identification of critical stages in the recruitment process of *J. macrocarpa*, together with factors influencing them, suggests some implication for management as well the hypotheses for future studies about conservation and recovery of the *J. macrocarpa* habitat.

Keywords Coastal dunes · Competition · Herbivory · *Juniperus* · Mediterranean habitat · Microhabitat

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Introduction

The transition period from seed germination to seedling establishment is a critical stage in the life cycle of vascular plants, and consequently a large number of studies have dealt with this issue (e.g. Harper 1977; Mendoza et al. 2009). Numerous biotic and abiotic factors constrain plant emergence, seedling survival and establishment, such as litter (e.g.

Molofsky and Augspurger 1992), light (e.g. Augspurger 1984), temperature (e.g. Callaway 1995), soil moisture (e.g. Dunne and Parker 1999), microhabitat (e.g. Gómez-Aparicio et al. 2005), microtopography (e.g. Huenneke and Sharitz 1986), seed arrival (Dalling et al. 2002), herbivory (e.g. Gómez et al. 2003), pathogens (e.g. Packer and Clay 2000) and competition with herbs (e.g. De Steven 1991). Moreover, seedling dynamics in Mediterranean ecosystems is conditioned largely by the particularities of the Mediterranean climate, such as the summer drought (e.g. Rey and Alcántara 2000), and the short duration of periods in which temperature and moisture are suitable for plant regeneration (Gulias et al. 2004).

In special environments such as coastal sand dunes, additional constraints for seedling establishment include water and nutrient stress, sand accretion and salt spray, as well as spatial and temporal variation in the dune substrate due to wind and wave action (Maun 1994). Besides environmental limitations for regeneration, coastal dune ecosystems are subjected to numerous types of anthropogenic impact such as trampling, off-road vehicle circulation and beach cleaning. In addition, the presence of recreational structures or touristic activities that limit and/or impede natural sand transport or alter the sand budget lead to severe erosion which is often permanent (Brown and McLachlan 2002; Defeo et al. 2009). In fact, the coastal ecosystems are among those most threatened in the Mediterranean Basin (EEA 1999). Specifically, the micro-forests dominated by *Juniperus macrocarpa* Sm. have been listed as priority habitats (2250 'Coastal dunes with *Juniperus* spp.') in the DIR. 92/43/EEC. This threatened habitat shows regeneration constraints and is often dominated by adult and senescent individuals of *J. macrocarpa* (Muñoz-Reinoso 2003), as in habitats characterized by other *Juniperus* species such as *J. communis* L., according to García et al. (1999), who pointed out that the conservation of this species in Mediterranean populations is due primarily to great individual longevity.

The regeneration problems for *J. macrocarpa* begin at the seed stage, since this species has low viability and germination percentage (Pacini and Piotto 2004; Juan et al. 2006; Pinna et al. 2014 in press). The low germination success is shared with other *taxa* such us *J. oxycedrus* L. (Ortiz et al. 1998) and *J. communis* (García et al. 2001). Germination can be delayed for

several years due to impermeable seed coats, embryo dormancy, or the presence of inhibitors (Chambers et al. 1999). In addition, predation of female cones and seeds by parasites limits seed viability in this genus (e.g. García 1998).

The next stage, from emergence to seedling establishment, has been studied for some species of *Juniperus* (e.g. Joy and Young 2002; Montesinos et al. 2007; Armas and Pugnaire 2009; Jovellar Lacambra et al. 2013). In most cases, low recruitment has been found, attributed not only to reproductive problems (e.g. Chambers et al. 1999; García et al. 2000) but also to other factors such as the summer aridity that may limit the survival of seedlings in Mediterranean environments (García et al. 1999), as well as in coastal dunes (e.g. Armas and Pugnaire 2009). However, few studies have explored the influence of environmental factors on seedling dynamics in *Juniperus* woodlands in dune ecosystems. Likewise, little is known about the initial phase in the life cycle of *J. macrocarpa*. In particular, Juan et al. (2006) performed a study using seeds from both mature and immature *J. macrocarpa* female cones, finding that substrate moisture was essential during seedling emergence.

In this study, we evaluated factors affecting the critical stages in the recruitment process of *Juniperus macrocarpa* seedlings. Specifically, we explored the influence of factors linked to seed source, herbivory, competition, and microhabitat conditions on emergence and mortality of *J. macrocarpa* seedlings with the aim of providing management tools for conservation and recovery of the fragile and threatened habitat characterized by this *taxon*.

Materials and methods

Study species and area

Juniperus macrocarpa is a dioecious species typical of coastal dunes in the Mediterranean region (Jalas and Suominen 1973; Amaral Franco 1986). Female individuals require two years to develop mature female cones, which are possible to find at different stages of maturity on the same plant simultaneously (Juan et al. 2006); ripening and dispersal of the female cones occur from autumn to spring (Pinna et al. 2014, in press). The tolerance to salt and sand-laden marine

winds (Géhu et al. 1990), the adaptation to substrate movements (García Novo and Merino 1993), and its important role in dune stabilization (Allier 1975), are also characteristic of this *taxon*.

The study was performed on the island of Sardinia, situated in the western Mediterranean basin (38°51′ and 41°15′ latitude north, 8°8′ and 9°50′ east longitude), covering c. 24,090 km^2. The total coastal length of the Island is 1,896 km, with 24 % (458 km) consisting of low, sandy or pebbly shores. Specifically, we selected four sites where the species is well represented, corresponding to four sites of community importance (SCI) of southern Sardinia (Porto Campana; Isola dei Cavoli, Serpentara, Punta Molentis e Campulongu; Is Compinxius-Campo dunale di Buggerru-Portixeddu and Da Piscinas Riu Scivu).

Sampling design and data collection

In the study area, 44 permanent plots of 1 × 1 m were randomly laid out (11 plots/site). For each plot, the global solar irradiation (annual W/m^2), was calculated based on data of exposure, slope, shade, coordinates, and mean transparency of the atmosphere recorded by the nearest weather stations in different periods of the year (Zangheri 1942; Gautam and Kaushika 2002).

Plots were monitored every three months, from April 2010 to January 2013 (12 monitoring events). All *J. macrocarpa* seedlings that have emerged were marked and the emergence date, the survival, and the growth (estimated from seedling height) were recorded. A microhabitat category was assigned to each seedling according to its location under a tree cover (canopy) or in open interspaces among woody vegetation (open). We also measured the following parameters for each plot: percentage of tree cover, percentage of shrub plus herbaceous cover (using a 10-cm grid cell), number of female cones on the soil, event number of herbivore-traces (including faeces, trampling, and cut plants). For the analysis, we estimated the mean values per plot of all these factors.

Data analysis

Linear mixed-effects model (LMM) was used to test the relative importance of different groups of explanatory variables on emergence, using the 'lme' function, which is included in the R nlme package (Pinheiro et al. 2011), while seedling survival was modelled by means of the 'glmer' function, included in the R lme4 package (Bates et al. 2012). Both functions fit LMM with specified mixtures of fixed and random effects. In particular, 'glmer' allows for non-normal errors and non-constant variance; thus, since survival is a binary response variable (dead or alive), we specified a binomial error distribution and the logit link function. The analyses were performed using the R 14.6 statistical package (R Development Core Team 2012).

We studied four factor types affecting seedling dynamics: 'seed source' (number of female cones), 'microhabitat' (using solar radiation to model emergence, and the categorical 'open/canopy' variable to model survival), 'competition' (shrub plus herbaceous cover), and 'herbivory' (herbivore-trace variable). Specifically, all four factor types were included as fixed effect to model seedling emergence, with the total number of new seedlings recorded in each plot from July 2010 used as the response variable. To test the relative importance of the explanatory variables on mortality, 'microhabitat', 'competition', and 'herbivory' factors were included as fixed effects, using the survival of all seedlings recorded from July 2010 as the response variable. The site factor was included as a random effect in all the models performed.

After fitting the full model for each response variable, we additionally considered reduced regression models and selected the most supported models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We performed automated model selection using the 'dredge' and 'subset' functions of the R-package 'MuMIn (Barton 2011), which calculates AIC values for models with all possible combinations of predictor variables and ranks them based on AIC. The relative importance (Burnham and Anderson 2002) of each predictor variable was then calculated based on AIC weights ('importance' function in 'MuMIn'). Throughout the text, means are followed by standard error.

Results

Seedling emergence

A total of 536 seedlings were marked from April 2010 to October 2012, 230 of which were in the plots before starting the sampling. Seedlings per plot ranged from 0

Fig. 1 Number of seedlings over the monitoring events. Total: cumulative curve including seedlings that were in the plots before starting the sampling. Emerged: Number of new seedlings in each period. Died: Number of seedlings died in each period. *Ap* April, *Ju* June, *Oc* October, *Ja,* January; -10: 2010, -11: 2011, -12: 2012
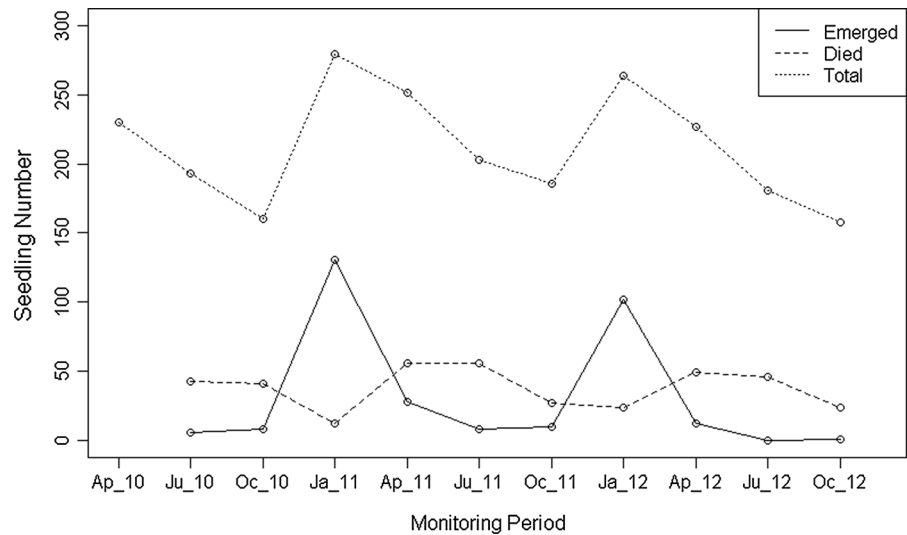

Table 1 Automated model selection based on multiple regression analysis on all subsets of a full model for seedling emergence

Models	Solar radiation	Fem cones	Herbivore-trace	HS cover	AIC	ΔAIC	AIC weight
1	–	n.i.	n.i.	n.i.	321.4	0.00	0.386
2	–	–	n.i.	n.i.	322.2	0.87	0.250
3	–	n.i.	–	n.i.	323.6	2.24	0.126
4	–	n.i.	n.i.	+	323.9	2.53	0.109
5	–	–	+	n.i.	324.9	3.58	0.065
6	–	–	n.i.	–	324.9	3.58	0.064
Importance	1.0000	0.3788	0.1904	0.1735			

Models were fit using LMM (maximum likelihood) with site as the random effect and fixed factors changing according to the specific model. Models are ranked according to Akaike's information criterion (AIC). Best models (ΔAIC < 4) are shown in detail, including the sign of regression coefficients, AIC, ΔAIC, and AIC weight. Additionally, relative variable importance of each variable in the most likely models (ΔAIC < 4) based on Akaike weights is shown

n.i. variable not included in model. Abbreviation of some fixed effects: *Fem cones* number of female cones, *HS cover* herbaceous plus shrub cover

to 91 (13.4 ± 2.56). A total of 306 seedlings emerged during the study, most of them in winter (Fig. 1), with winter 2010 being particularly favourable for emergence (131 seedlings). However, a few seedlings emerged also in the other seasons.

Regarding the factors explaining seedling emergence, significant differences were found in the explanatory power of each of the factors included in the full model, with the microhabitat effect being the most relevant (Table 1). Specifically, the number of emerged seedlings decreased with solar radiation in all best models (ΔAIC < 4). The model including only this explicative variable did not improve after adding other fixed terms.

Seedling survival and early growth

For the 306 new seedlings that emerged from July 2010 through the remainder of the study, 232 seedlings died by January 2013, with the survival percentage being 24.18 %. For the specific cohort of the 131 seedlings that emerged in January 2011, 111 died by January 2013, with the survival percentage being 15.27 %. Most of the seedlings died in the first few months after emergence (i.e. 33.6 % of the seedlings had died by April), reaching the highest mortality percentage in the first summer (Fig. 2). After this season, the mortality percentage dropped, but it picked up in the second summer. Data on the cohort that

Fig. 2 Mortality percentage over the monitoring events for January 2011 cohort, calculated as the ratio between seedlings that died and those that remained alive in the specific monitoring period. *Ap* April, *Ju* June, *Oc* October, *Ja* January; -11: 2011, -12: 2012
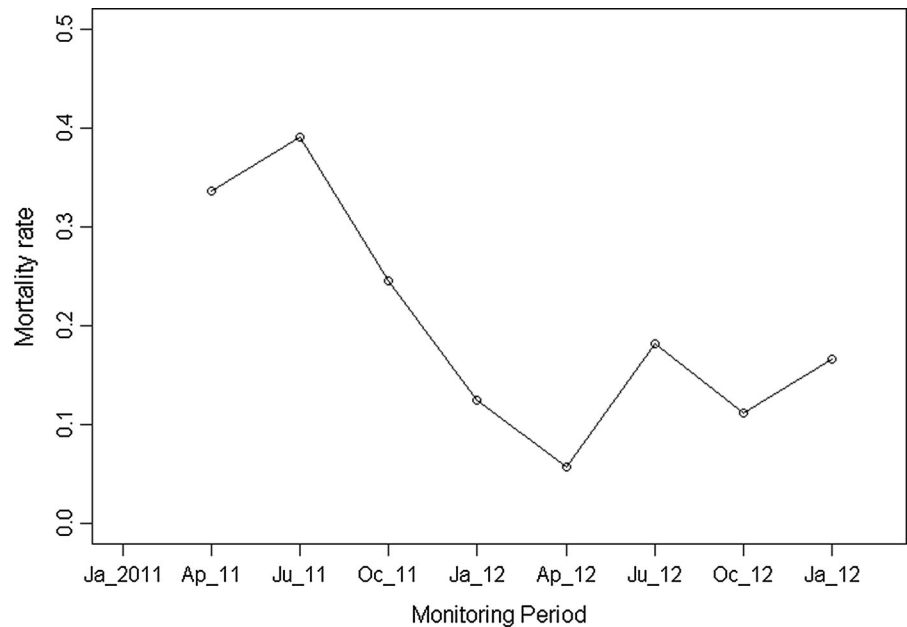

Table 2 Automated model selection based on multiple regression analysis on all subsets of a full model for seedling mortality

Models	Open microhabitat	Herbivore-trace	HS cover	AIC	ΔAIC	AIC weight
1	+	+	−	318.5	0.00	0.551
2	+	+	n.i.	319.5	1.00	0.334
3	n.i.	+	−	321.6	3.13	0.115
Importance	0.8848	1.0000	0.6659			

Additional information is provided in Table 1

emerged in January 2012 showed a similar early trend. Thus, the three minima in the cumulative curve of seedlings were recorded in October (Fig. 1), with the number of living plants progressively decreasing from the emergence time to late summer.

Among the factors explaining seedling mortality, the relative importance of herbivory was the highest, while the microhabitat effect was also relatively important (Table 2). In particular, in the optimal model seedling mortality increased with herbivore-traces and being located in open interspaces, but decreased with herbaceous plus scrub cover.

In January 2013, the mean height growth for the surviving seedlings that emerged in January 2011 was 4.73 ± 0.40 cm (maximum 8.5, minimum 2.0 cm); although due to the low number of surviving seedlings, it was not possible to fit the models explaining growth.

Discussion

Seedling emergence

Our results suggest that seedling emergence of *Juniperus macrocarpa* depended on temporal, as well as environmental factors. The timing of seedling emergence is one of the key events in the life cycle of plants that determine plant performance and success (Harper 1977). Specifically, we found that most of the seedlings emerged in winter, although we recorded seedling emergence in all seasons. According to local climatic conditions and our own results (e.g. Pinna et al. 2014, in press), *J. macrocarpa* seeds are able to germinate throughout seed dispersal during the rainy seasons, from autumn to the beginning of spring. In fact, the high number of new emerged seedlings

recorded in January had germinated in autumn and in the early winter. Winter emergence represents an advantage, since the seedlings benefit from the moist conditions of the mild winter (characteristic of the study area) and the following spring (Skordilis and Thanos 1995; Thanos 2000). By contrast, we found a very low number of new seedlings in summer and in the early autumn, as expected, but also in spring. However, in all seasons, a higher number of *J. macrocarpa* seeds probably germinated, although the potential seedlings could die before being recorded as emerged individuals. The low seedling emergence recorded in spring, when the temperature is usually optimal for germination, but water availability is declining, suggests that drought is the most limiting factor in seedling emergence, in agreement with previous studies performed in Mediterranean environments (e.g. Gulias et al. 2004).

This finding is also consistent with our results concerning the models performed to explain seedling emergence, since microhabitat was the most important factor. In particular, the negative relation found between number of emerged seedlings and solar radiation suggests that in areas shielded from sunlight, emergence is promoted by positive microsite effects, this finding being consistent with previous data on *Juniperus* (e.g. Van Auken et al. 2004; Jovellar Lacambra et al. 2013). The strength of solar radiation depends on exposure and slope, but also being filtered under the tree canopy is a key factor. In areas sheltered from the solar radiation, seedlings undergo more favourable water relations, due to lower evaporative demand and temperature (De Jong and Klinkhamer 1988). Particularly for *J. macrocarpa*, Juan et al. (2006) also found higher seedling emergence under shaded/watered conditions. Similarly, higher number of woody seedlings has been found under other species of *Juniperus* trees in dune systems of North America (Joy and Young 2002); in particular, they showed that radiation was reduced and soil-temperature fluctuations were moderated under *J. virginiana* L., while values of edaphic variables favouring seedling development, such as moisture content and organic matter, were higher under trees than in exposed sites. The positive effect of the canopy for seedling emergence has been repeatedly shown in other Mediterranean environments (e.g. Lloret et al. 2005).

Contrary to what would be expected, more female cones, and therefore, more seeds, do not guarantee higher seedling number. This fact, may be related to the low germination and viability percentage found for this species (Pinna et al. 2014, in press), but also to the importance of seeds that reach appropriate microhabitats (e.g. Chambers et al. 1999). The activity of birds in relation to dispersion and emergence could be also a key factor in seedling dynamics of this species, as has been demonstrated for other *Juniperus* species (García 2001).

Seedling survival and early growth

Seedling survival in this study proved very low, c.a. 15 % for a specific cohort, and therefore, seedling survival could be the most limiting factor in the recruitment process. Consistently, low survival percentages have been related to other species of *Juniperus* (García et al. 1999; Van Auken et al. 2004), as well as other species of dune environments (Maun 1994; Cogoni et al. 2013a). The highest emergence was reached in January and most of the seedlings died in the first months after emergence, reaching the highest mortality percentage in the first summer, this trend being typical of Mediterranean ecosystems (e.g. Giménez-Benavides et al. 2007; Mediavilla and Escudero 2010), as for various *Juniperus* species (e.g. Jackson and Van Auken 1997; García et al. 1999; Armas and Pugnaire 2009). However, to overcome the first summer did not guarantee the definitive seedling survival. Thus, seedlings continued dying, although progressively in lower proportion, registering a new mortality peak in the second summer, as reported for other species in Mediterranean context (e.g. Herrera et al. 1994; Mendoza et al. 2009).

Furthermore, we found that survival of *J. macrocarpa* seedlings was related to herbivory and competition. Specifically, herbivore-trace was positively related to seedling mortality, in agreement with Fisher et al. (1990) and García et al. (1999). Conversely, herbivory did not significantly affect seedling survival in some other *Juniperus taxa* (Jackson and Van Auken 1997; Joy and Young 2002; Montesinos et al. 2007), suggesting that limited palatability of junipers may restrict herbivory. In fact, we did not observe many cropped seedlings, but we found mainly traces of trampling by goat and deer, as well as faeces of rabbit and hare. In addition, we sporadically found fox faeces, which may influence not only trampling but also seed dispersion.

Also, seedling location in open interspaces among woody vegetation increased the risk of seedling

mortality, as expected, since higher radiation involves high temperatures and loss of soil moisture (Joy and Young 2002). Moreover, herbaceous plus scrub cover was negatively related to *J. macrocarpa* seedling mortality. In this sense, Armas and Pugnaire (2009) also found that survival of *J. phoenicea* L. seedlings was enhanced beneath shrubs, especially under clumps, in a coastal sand-dune system. Similarly *J. occidentalis* Hook. seedlings became established most readily in areas with well-developed herbaceous and shrubby vegetation (Burkhardt and Tisdale 1976). Therefore, our results suggest that shrubs provide a microclimatic benefit rather than a competition constraint, since shading by shrubs can reduce soil–water evaporation (Pugnaire et al. 2004).

Our findings confirmed that *J. macrocarpa* is a slow-growing species, at least in the seedling stage, as has been verified for other species of this genus (e.g. Ortiz et al. 1998; Jovellar Lacambra et al. 2013). Specifically, we found that the growth of surviving plants in no case exceeded 8.5 cm, after two years and therefore, as expected, no seedling reached the subsequent size class, defined for individuals over 25 cm (Ward 1981; Clifton et al. 1997). In fact, also from an age standpoint, all individuals remained seedlings, since young plants (next age class), has been defined in this genus for individual between 6 and 20 years (Ward 1982; Clifton et al. 1997). Our results did not allow us to analyse factors influencing early growth because most of the seedlings died during the first months from emergence and, therefore, few seedlings remained to be evaluated. Indeed, factors influencing early seedling growth in the genus *Juniperus* have been poorly studied (e.g. Miller and Rose 1995; McKinley and Van Auken 2005).

Implication for recovery and conservation

In conclusion, we found that the recruitment of *J. macrocarpa* is highly limited in the initial phases of its life cycle. Firstly, seed viability and germination are very low. Moreover, the emergence season is limited almost exclusively to autumn and winter, although both the ripening and dispersal period of female cones, as well as the potential period for germination are longer (Pinna et al. 2014, in press). In addition, we found microhabitat and herbivory constraints in seedling dynamics. Thus, besides emergence limited to particular microhabitat conditions (being the number of seedlings negatively linked to areas sheltered from solar radiation), a very low survival percentage was found, with the highest mortality percentage recorded in the first summer and linked to herbivore-trace and location in open interspaces. Furthermore, the few surviving seedlings grew slowly, in no case exceeding 8.5 cm after two years.

The identification of critical stages in the recruitment process of *J. macrocarpa,* together with factors influencing them, suggests some implication for management, as well the hypotheses for future studies about conservation and recovery of the fragile and threatened habitat of which this *taxon* is an essential part. Specifically, our results suggest that planting could be a more effective option than sowing, since limitations for both germination and emergence could be overcome under greenhouse conditions. In any case, if sowing is the option, it should be performed applying techniques such as organic blanket, which reduces evaporation and promotes higher seedling density in harsh environments (Ballesteros et al. 2012). In addition, successful *J. macrocarpa* planting could be improved using a shelter tube with lateral ventilation, appropriate for Mediterranean conditions, since it could increase growth (Jiménez et al. 2005), and protect seedling against direct radiation and evapotranspiration. It would be advisable to place protections against herbivores in problem areas. Moreover, we found no competition problems, and therefore, removing herbaceous or scrub cover is not recommended. Finally, both planting and sowing should be undertaken in autumn, which has been shown to be an advantageous period for plant reintroduction in Mediterranean dunes (Cogoni et al. 2013b), since seeds and seedlings could benefit of the moist conditions before summer drought.

Conflict of interest The authors declare that they have no conflict of interest.

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