RESEARCH PAPER

Recruitment pattern in an isolated small population of the Mediterranean dwarf shrub *Satureja thymbra* L. and implication for conservation

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Abstract

The recruitment pattern of *Satureja thymbra* (Lamiaceae), in a single and isolated population in Sardinia, was experimentally investigated by human-mediated sowing in the field: 12 plants in two habitats (inside and outside of "phrygana" habitat) were randomly selected as the source of seeds and a total of 2160 seeds were buried in two microhabitats, under the canopy and in open areas (3 replicas × 30 seeds × 12 plants × 2 microhabitats). The experiment was monthly monitored over a 2-year period. Germination and recruitment of *S. thymbra* were extremely low. Significant differences in the interaction among habitat and cohorts in seedling emergence were found. Differences between cohorts are due to the early emergence, which protected seedlings from seasonal drought. Seedling emergence in both microhabitats was recorded, although no significant differences were found. Additionally, significant differences in survived seedlings for habitat and cohort and for the interaction among them were found. The phrygana habitat showed a positive effect on the persistence of *S. thymbra*, by protecting plants from human disturbance, hence its conservation is essential to increase the population size of *S. thymbra*. Our findings, increasing the knowledge of the recruitment pattern of *S. thymbra,* provide also useful information for its conservation.

Keywords Habitat · Facilitative effect · Isolated plant population · Sardinia · Lamiaceae

1 Introduction

Mediterranean-type ecosystems are subjected to harsh climatic conditions such as summer drought and high temperatures (Géhu 1986; Callaway 1995; Thompson 2005; Quézel and Médail 2017). In these ecosystems, interactions among plant communities generally change according to the stress-gradient hypothesis. In particular, environmental stress can changes consistently when facilitation (typical of survival responses) or reduction in the competition (typical of growth and reproduction responses; He et al. 2013) occur. Specifically, in these ecosystems, dominant perennial plants cause changes in micro-climate and soil properties, leading to the formation of "fertile islands" under plant canopies with a consequent facilitating effect (He et al. 2013; Gómez-Aparicio et al. 2005; Pugnaire et al. 2011; Navarro-Cano et al. 2015). In such conditions, the established vegetation may offer protection to seedlings by buffering microclimatic extremes (i.e., reducing solar radiation and soil temperature, conserving soil moisture, and enriching nutrient content) and may protect seedlings from herbivore damage (Callaway 1995; He et al. 2013; Gómez et al. 2001; Fenu et al. 2017; Andivia et al. 2017). These forms of protection play an important role in seedling dynamics especially for seedling survival and establishment (Rey and Alcántara 2000; Gulias et al. 2004; Cogoni et al. 2012), which represent a critical phase in inhabiting arid environment under a typical Mediterranean climate (Cogoni et al. 2012). In these contexts, characterized by a highly seasonal alternation of suitable and unfavourable conditions, survival and establishment stages must take place in a window of favourable conditions, which might vary in length, and in which environmental cues and constraints play a central role (Cogoni et al. 2012; Thanos et al. 1995). Seed germination and the transition from seed

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206

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

to seedling are also high-risk periods in the life cycle of most plants (Cogoni et al. 2012; Mendoza et al. 2009; Sulis et al. 2018), and seedlings are the most vulnerable stage of the life cycle of plants, being subjected to several abiotic and biotic constraints that may affect their emergence, survival and establishment (Cogoni et al. 2012, 2013; Mendoza et al. 2009; Moles and Westoby 2004; Leck et al. 2008).

The individual growth, survival and reproductive output of plant populations can vary largely throughout the geographical range of a species (e.g. Castilla et al. 2011; Giménez-Benavides et al. 2007; Yakimowski and Eckert 2007; Sulis et al. 2017). In the Mediterranean Basin several cases of consistent disjunction in the distribution range of plant species, showing peripheral populations isolated from the main home range, were documented (e.g. Gargano et al. 2007; Pouget et al. 2013; Sulis et al. 2020). Isolated populations, having biological and ecological requirements that may differ, even considerably, from those typical of the populations located in the "core" distribution, represent per se interesting targets in ecology, evolutionary biology and genetics (e.g. Sexton et al. 2009; Pouget et al. 2013; Sulis et al. 2017, 2020). In addition, another peculiarity of several plant species in the Mediterranean Basin is that isolated small populations occur within natural areas, often near or inside urban areas (Gargano et al. 2007; Sulis et al. 2020; Itani et al. 2020); this situation usually represents a threat factor being the urban sprawl the leading cause of species endangerment. In fact, urban development negatively impacts biodiversity through land disturbance, removal of native vegetation, the introduction of exotic species, and fragmentation and isolation of remaining natural areas (Bryant 2006; Widawski and Jary 2019). Furthermore, in natural areas the common nature-based activities, such as hiking, often have consistent impacts on vegetation, causing crushing, shearing off and uprooting of plants as well as the loss of height, biomass, reproductive structures, and reduction in cover, increased litter, and damages to seedlings and changes in species composition (Pickering and Hill 2007; Pickering et al. 2010; Ballantyne and Pickering 2015).

The complex interaction with these peculiar factors, shared by several populations of plant species along the Mediterranean Basin, contributes to considerably affect the recruitment pattern in the wild. In this paper, we investigated the recruitment pattern of *Satureja thymbra* L. (savory of Crete or Whorled savory; Lamiaceae family) in Sardinia, as a typical example of an isolated population growing in a natural area located within an urban context (San Michele hill, Cagliari municipality). *Satureja thymbra* is present in Sardinia in a single and isolated population, completely separated from the distribution range of this species centred in the eastern Mediterranean Basin (Martinoli 1950; Pinna et al. 2015), which represents the westernmost part of its distribution range population. Therefore, *S. thymbra*

is a plant of phytogeographic interest both at the Italian and Sardinian level.

The main threats affecting the species in Sardinia are linked to recreational human activities, which provoke the opening of new paths and a general continuous loss of habitat quality; in addition, the management practices carried out in this urban natural area and the recurrent mowing of natural vegetation (mainly aimed at fire prevention) cause the elimination of seedlings and severe limitations to the recruitment of new individuals (Pinna et al. 2015). The main aim of this research was to characterize the recruitment pattern of *S. thymbra* at a small scale in the isolated population occurring in Sardinia. The results of this study also provide useful information for planning a specific conservation project to preserve this small population of the species *S. thymbra*.

2 Materials and methods

2.1 Study species

Satureja thymbra L. is a dwarf shrub, grayish-pubescent, covered by glandular trichomes, with leaves linear-lanceolate, opposite and puberulous and many-flowered verticillasters. The calyx is tubular, bell-shaped, the corolla is glabrous, pink or red–purple, ovary with bifid stigma, the fruit is a 4-parted schizocarp with spherical and glandular achenes (Pinna et al. 2015; Pignatti et al. 2017). Flowering occurs from February to June (from February to April in Sardinia), and fruiting from May to July (Pinna et al. 2015). *Satureja thymbra* is also an aromatic plant, which produces essential oils used for biological activities (Dell'Agli et al. 2012). The essential oils inhibit the germination of seeds, dispersed within fruiting calyces, resulting in a consequent diaspore dormancy, which is overcome by the leaching of inhibitors with rainwater (Ibáñez and Schupp 2001).

Satureja thymbra is a heliophilous and xerophilous plant species mostly distributed in the eastern Mediterranean Basin (Crete, Cyprus, Greece, Israel, Italy, Jordan, Lebanon, Libya, Palestine and Turkey (Euro + Med PlantBase 2020). The westernmost population, extremely small in size and completely isolated by the nearby populations, occurs in an urban natural area located within the city of Cagliari (Sardinia). Specifically, *S. thymbra* population grows on the San Michele hill and it consists of two adjacent nuclei located in the NE and NW slopes (Fig. 1; Pinna et al. 2015). San Michele hill is a calcareous relief with a maximum elevation of 120 m a.s.l., constituted by the formation of Miocene age (Pinna et al. 2015), a compact limestone formation with clayey soil characterised by a particular type of substrate with a high content of magnesium salts and poor concentration in ferrous and ferric salts (Biondi and Mossa 1992). Available climatic data from the Cagliari weather station

Fig. 1 Aerial photograph of the study area and position of *S. tymbra* individuals selected for the recruitment experiment in San Michele Hill (urban area of Cagliari, Sardinia). Green circles indicate plants growing within the phrygana habitat; red triangles indicate isolated plants growing out of the phrygana habitat (colour figure online)
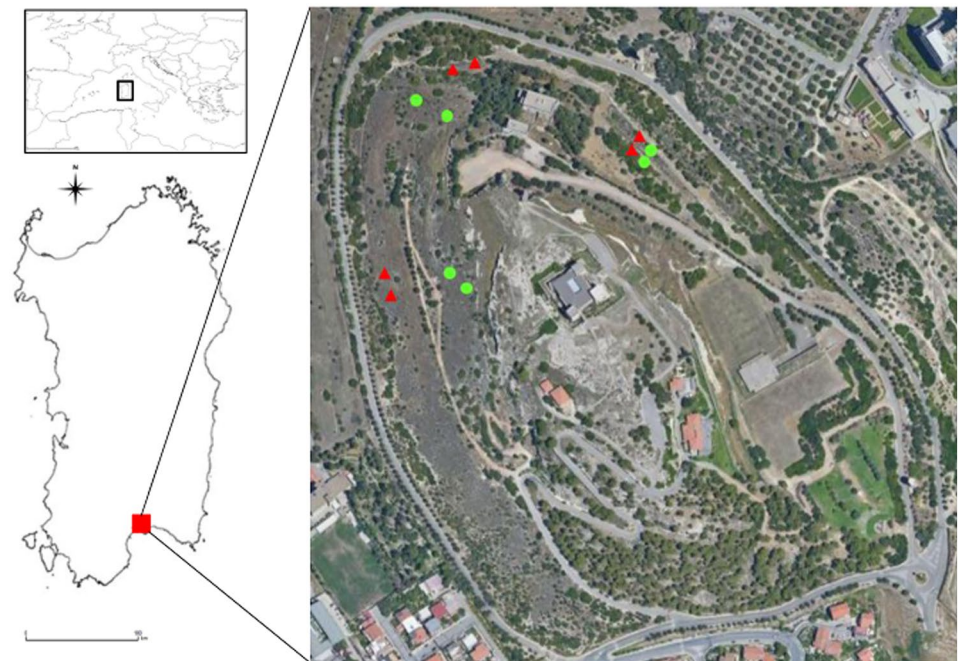
indicate a typical Mediterranean annual pattern of temperature (annual mean: 17.9 °C) and precipitation (annual mean: 394 mm). Bioclimatically this area occurs in the Mediterranean pluviseasonal oceanic bioclimate, with upper thermomediterranean thermotype and upper dry ombrotype (Pinna et al. 2015). In the study area, *S. thymbra* represents one of the structural species of the typical *phrygana* habitat referred to *Thymelaeo hirsutae–Thymetum capitati* Biondi and Mossa 1992 (Biondi and Mossa 1992).

Given the small extent of the area of occupancy, the small population and the continuous decline in habitat quality, *S. thymbra* was assessed as critically endangered at the regional level according to the IUCN protocol (Pinna et al. 2015).

2.2 Sampling design

The recruitment pattern of *S. thymbra* was investigated considering two levels corresponding to the population structure: habitat and microhabitat. Specifically, due to the spatial distribution of *S. thymbra* individuals, two different habitats were selected: (1) plants growing within a structured and continuous phrygana habitat ("PAH") and (2) isolated plants growing out of the phrygana habitat ("ISP"; Fig. 1).

In addition, following the same approach in Fenu et al. (2017), we identified two microhabitats, "canopy" and "open". The first includes the space under the canopy of individual maternal shrubs, where *S. thymbra* seedlings would benefit from amelioration of the environmental conditions and physical protection against trampling. The second includes all surfaces not covered by *S. thymbra* plants

(i.e. the interspaces near the maternal individuals, without interaction between these and the seedlings).

2.3 Seedling emergence and survival

Seedling emergence and survival were experimentally investigated by human-mediated sowing in the field. In August, 12 maternal plants equally distributed in two different habitats ("PAH" and "ISP"; Fig. 1) were randomly selected as the source of seeds. The source plants were near each other and shared similar soil properties and microclimatic conditions. Seeds were collected, cleaned and, after removing all non-viable seeds, separately stored in the laboratory under controlled conditions. To simulate the more natural conditions in this experiment, we did not carry out laboratory germination tests or applied pre-treatments in the collected seed lots.

The procedure was completed at the beginning of September. Soon after, 12 sowing sites were established in correspondence to the maternal plants, six in PAH and six in the ISP habitat. Within each habitat, three sowing sites corresponded to the "canopy" and three to the "open" microhabitat. The sowing time was selected according to previous studies indicating that although seeds of this species (and other Mediterranean Lamiaceae species such as *Origanum vulgare* subsp. *viridulum* (Martrin-Donos) Nyman) ripe in summer they are mainly dispersed at the beginning of the rainy season (Thanos et al. 1995; Kadis and Georghiou 2010; Thanos and Doussi 1995), usually in early March. Accordingly, the germination studies in the laboratory, carried out by Bocchieri et al. (2000), showed a high

208

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

germination percentage at the optimal temperature of 16 °C. Likely, the absorption of moisture promotes the opening of the calyces, and the germination of the seed, under relatively low temperatures (Thanos et al. 1995; Kadis and Georghiou 2010; Thanos and Doussi 1995).

In each sowing site, six circular aluminium pots with a diameter of 8.5 cm, were placed in two microhabitats: three pots under the canopy ("canopy") and other three in the interspace near the shrubs ("open"). Within each pot, 30 seeds were homogeneously distributed and sown (3 replicas × 30 seeds × 12 maternal plants × 2 microhabitats; a total of 2160 seeds; Fig. 2), after visually checking the quality of all seed-lots.

Seeds were buried in the clayey soil at a specific depth calculated according to the allometric correlation between the maximum depth at which seedling emergence occurs and the seed mass [maximum depth (mm): $27.36 \times$ seed weight $^{0.334}$ (mg)] found by Bond et al. (1999); finally, each replica was covered by a fine mesh net to avoid the addition of new seeds dispersed both from the maternal plant and nearby individuals.

Each site was monthly monitored over a 2-year period. All seedlings that emerged during the same year were considered as a member of the same cohort. At the end of the first year, all emerged seedlings belonging to the cohort I were explanted, and each replica was re-covered by a mesh to avoid contamination by other dispersed seeds. Then, during the second year all newly emerged seedlings of cohort II were monitored until the end of the study period. During the monitoring activities, emergence and survival were recorded for each seedling by using a binary scale (1–0).

2.4 Data analysis

The emergence proportion was calculated by dividing the number of seedlings that emerged in each cohort by the total number of seeds sowed.

To evaluate the effect of habitat, microhabitat, and cohort on seedling emergence and survival, two independent generalized linear models (GLMs) were performed by a stepwise procedure. Post-hoc tests for pairwise comparisons were done by Tukey's honestly significant difference test (HSD).

The non-parametric Kaplan–Meier method was used to estimate the survival function directly from the survival times in our survival data set. Afterwards, to compare the differences in the survival functions between cohorts, the Gehan's Wilcoxon test, was performed.

All statistical analyses were performed using Statistica 8.0 software (Statsoft, USA).

3 Results

An extremely low number of seedlings (16 in total of the 2160 seeds sown) emerged during the 2-year study period. Six of 16 emerged seedlings died in the first summer, and seven in the second summer, while only three survived (Table 1).

In cohort I, eight seedlings emerged in April, six of which died within summer, reaching the highest mortality in July, with a total survival percentage in the cohort being 25%. In cohort I, all emerged seedlings were in the "canopy". In cohort II, eight new seedlings emerged in February: seven died in July, while only one survived until August (Table 1). Compared to cohort I, in cohort II seedlings emerged in both microhabitats (canopy and open), specifically, five in open and three in the canopy, 62.5% and 37.5%, respectively.

The number of emerged seedlings differed in two habitats, depending on the cohort; in particular, in cohort I seedlings emerged in both habitats: PAH and ISP (87.5% and 12.5%, respectively), while in cohort II all seedlings emerged in ISP. The overall emergence was extremely low (0.37% of the seeds sowed).

Fig. 2 Three replica × 30 seeds (**a**) were sown in circular pots for each microhabitat "canopy" and "open", respectively (**b**)

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

209

Table 1 Total emerged, dead and survivor seedlings over the monitoring events during cohorts I and II in the two microhabitats (canopy and open factor) and habitat (ISP and PAH)

	ISP		PAH		Total emerged	Total dead	Total survivor
	Canopy	Open	Canopy	Open			
Cohort I	1	–	7	–	8	6	2
Cohort II	3	5	–	–	8	7	1

The seedling survival was higher in cohort II. In particular, average seedling survival was $0.56 \pm 0.16\%$ (Kaplan–Meier estimates $\pm$ SE) in cohort I, with 5 seedlings survived after 5 months and died in the 7th month; while in cohort II the average survival percentage was $0.50 \pm 0.15\%$ (Kaplan–Meier estimates $\pm$ SE), with 7 seedlings survived after 5 months and died the 6th month. The comparison of the survival percentages showed significant differences between the 2 cohorts ($p < 0.01$ by Gehan's Wilcoxon test).

The GLM analysis for seedling emergence (Table 2) showed significant differences in the number of emerged seedlings for the interaction among habitat and cohort ($p < 0.05$). Conversely, no significant differences in the number of emerged seedlings per habitat, microhabitat, and cohort were found. In addition, there were no significant differences in the number of emerged seedlings for the interactions between microhabitat and habitat, microhabitat and cohort, as well as the interaction among microhabitat, habitat and cohort.

The GLM analysis for seedling survival (Table 2) showed significant differences in the number of survived seedlings per habitat and cohort and for the interaction among them ($p < 0.05$), whereas no significant differences in the number of survived seedlings for microhabitat and the interaction among microhabitat, habitat and cohort were found. The HSD Tukey test highlighted significant differences between PAH and ISP (approximate probabilities for post-hoc tests error: between MSE = 0.1593, $df = 142.00$; $p = 0.039$) and the interaction between habitat and cohort on seedling survival (Table 3).

Table 2 Generalized linear models (GLMs) results for the effect on seedling emergence (deviance: 37.04; Pearson Chi^2: 37.04; logLik: − 106.57) and survival (deviance: 37.04; Pearson Chi^2: 37.04; logLik: − 106.57) of habitat, microhabitat and cohort

	SS	DF	MS	F	p value
Seedling emergence					
Intercept	2.1701	1	2.1701	7.9678	0.0055**
Microhabitat	0.0868	1	0.0869	0.3187	0.5733 NS
Habitat	0.4201	1	0.4201	1.5426	0.2164 NS
Cohort	0.1701	1	0.1701	0.6247	0.4307 NS
Microhabitat × habitat	0.2812	1	0.2812	1.0326	0.3113 NS
Microhabitat × cohort	0.5868	1	0.5868	2.1545	0.1445 NS
Habitat × cohort	1.5312	1	1.5312	5.6220	0.0191*
Microhabitat × habitat × cohort	0.0035	1	0.0035	0.0127	0.9103 NS
Error	37.0417	136	0.2724		
Seedling survival					
Intercept	1.1250	1	1.1250	7.2857	0.0078**
Microhabitat	0.0139	1	0.0139	0.0899	0.7647 NS
Habitat	0.6806	1	0.6806	4.4074	0.0376*
Cohort	0.6806	1	0.6806	4.4074	0.0376*
Microhabitat × habitat	0.1250	1	0.1250	0.8095	0.3699 NS
Microhabitat × cohort	0.1250	1	0.1250	0.8095	0.3699 NS
Habitat × cohort	1.1250	1	1.1250	7.2857	0.0078**
Microhabitat × habitat × cohort	0.0139	1	0.0139	0.0899	0.7647 NS
Error	21.0000	136	0.1544		

NS not significant, *SS* sum of squares, *DF* degrees of freedom, *MS* mean square, *F* F test

*$p < 0.05$; **$p < 0.01$

210

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

Table 3 Post-hoc HSD Tukey test for habitat (PAH and ISP factors) and cohort (cohort I and II) on seedling survival (approximate probabilities for post hoc tests error: between MSE = 0.161, df = 139.00)

Variables	PAH×cohort I	PAH×cohort II	ISP×cohort I	ISP×cohort II
PAH×cohort I		0.9570 NS	0.9759 NS	0.0190*
PAH×cohort II	0.9570 NS		1.0000 NS	0.0049**
ISP×cohort I	0.9759 NS	1.0000 NS		0.0209*
ISP×cohort II	0.0190*	0.0049**	0.0209*	

NS not significant

*$p < 0.05$; **$p < 0.01$

4 Discussion

The germination and recruitment final percentages of *S. thymbra* recorded in the isolated Sardinian population were extremely low with an exiguous number of seedlings emerged over a 2-year of study. However, previous seed germination tests carried out using *S. thymbra* seeds collected in the same population showed that the species is able to germinate, at a constant humidity and temperature (16 °C), reaching germination percentages higher than 80% (Bocchieri et al. 2000). These differences between the germination results achieved in the natural environment and in lab-controlled conditions, might be explained, on the one hand, by the Mediterranean climate, characterized by a highly seasonal alternation of favourable and unfavourable conditions. In this climate, plant reproduction must occur in a restricted window of favourable conditions that may vary in length and in which environmental cues and constraints play a central role (Thanos et al. 1995; Pinna et al. 2014). On the other hand, seedling emergence and recruitment in *S. thymbra* could be also largely conditioned by water availability. This is linked to the particularities of the specific condition of the typical Mediterranean climate, such as the prolonged summer drought that is one of the most limiting factors in seedling emergence (Rey and Alcántara 2000; Cogoni et al. 2012; Gulias et al. 2004). Therefore, water availability seems to be the crucial factor for *S. thymbra* germination and seems to be the reasons for the failure of *S. thymbra* germination in the field observed in this study and, conversely, the higher germination in laboratory tests.

The absence of periodic fires in the area where the *S. thymbra* population occurs might be another limiting factor that caused the low germination percentages obtained in our study. In fact, it has been demonstrated that smoke and fire play an important role in promoting the seed germination and seedling emergence of *S. thymbra* (Çatav et al. 2012, 2014). The role of fire-related cues (heat and smoke) in the stimulation of germination in many plants is well known and it has been demonstrated in several fire-prone Mediterranean ecosystems (e.g. Keeley and Bond 1997; Herranz et al. 1998; Moreira et al. 2010; Moreira and Pausas 2018; Çatav et al. 2018; Golan et al. 2019). In particular, fire-enhanced germination allows several species belonging to the Lamiaceae, a family containing resins, terpenes and other volatile substances, to persist in frequently burned Mediterranean habitats (Çatav et al. 2018), also the seedling emergence and growth is enhanced by at least one of the fire-derived chemicals and therefore the recruitment of several Mediterranean species might be enhanced by different smoke compounds (Çatav et al. 2018). In fact, in post-fire environments, the early appearance of seedlings may give an advantage to a species to outcompete the others, therefore, the faster germination rate of *S. thymbra*, possibly contributes to the establishment success of this *taxon* after the fire (Çatav et al. 2014).

The low germination percentages observed in our short-term study (2 years) could be also negatively influenced by the ability of this plant to implement a permanent soil seed bank, as the seeds produced in a specific year can enter the soil seed bank and are able to germinate after several years (Çatav et al. 2014; Cerabolini et al. 2003). It contributed to the low germination recorded having covered the replica by a fine mesh, used to avoid contamination by new other dispersal seeds, which may have concurred to a smaller number of dispersed seeds and, consequently, of total emerged seedlings.

A further indication that the seeds have several limitations to germinate in the San Michele hill is indirectly provided by historical information on the population; in fact, the low recruitment seems to be supported by some observations reported in the literature indicating a constant surface-area occupied by the population over time without any significant change in its size besides the fact that the species did not spread to the nearby hilly areas characterized by the same calcareous substrate. (Martinoli 1950; Bocchieri et al. 2000; Biondi and Mossa 1992).

In terms of seedling emergence, according to Cogoni et al. (2013), which proved that the emergence depends on the timing and is influenced by the habitat where seedlings grow, we found significant differences in the interaction among habitat and cohorts as concerns seedling emergence.

Our results seem to confirm that the early time of seedling emergence influences the survival differences between the cohorts. Many studies showed that early seedlings have been favoured over later ones in survival and growth since plants emerging at the beginning of the rainy season have a higher probability of survival, greater availability of resources, and more time to establish before seasonal drought (Cogoni et al. 2013; Weekley et al. 2007; Turkington et al. 2005).

The interaction among habitats and cohorts in seedling emergence seems to be linked to the fact that, in our experiment, seedlings emerged in both habitats, but in different time between cohorts. In fact, in cohort II the emergence in the early rainy season allowed to be recorded the same number of seedlings emerged, also outside the phrygana habitat.

In complex environmental contexts such as the Mediterranean areas, the facilitative mechanisms among plants could be crucial for the persistence of several plants, for which survival is linked to a fragile equilibrium with the surrounding microenvironment (He et al. 2013; Gómez et al. 2001; Andivia et al. 2017). In fact, increased seedling survival under nurse plants has been demonstrated in several Mediterranean contexts (Andivia et al. 2017; Mendoza et al. 2009; Cogoni et al. 2013). However, we recorded seedling emergence in both microhabitats, although no significant differences were found. Seedling protection is expected under the canopy because of several factors such as amelioration of microclimatic conditions, or reduction of water stress and protection of trampling among others (Fenu et al. 2017; Pinna et al. 2014; Ibáñez and Schupp 2001; Schenk and Mahall 2002).

The seedlings' survival was significantly influenced by the habitat (inside or outside phrygana habitat). Our results showed that phrygana had a positive effect on the persistence of *S. thymbra* isolated population since played a major indirect role by protecting plants from human trampling.

Considering that timing of emergence is one of the most important factors affecting seedling survival (Howell 1981; Cogoni et al. 2013; Pinna et al. 2014), our results seem to confirm that differences in percentages between the cohorts are related to the early time of seedling emergence. Conversely, in this study, the highest survivorship was recorded in cohort II when the seedlings emerged in April. Even the interaction between habitat and cohorts had significant effects on seedlings' survival. In particular, the survival of seedlings that emerged in the most favourable period (at the beginning of the rainy season), but outside the phrygana was influenced by the habitat in which they grew. Therefore, the survival of seedlings varied significantly according to the cohorts, confirming the importance of phrygana habitat on the persistence of *S. thymbra*.

In conclusion, our results suggested that the recruitment strategy of *S. thymbra* seems to be linked to a long-lasting soil bank and to environmental factors, like availability of water and fire, these latters inasmuch can break the dormancy of seeds. Therefore, *S. thymbra* follows the typical pattern of a long-lived Mediterranean perennial species, which are generally characterised by populations with adult individuals and extremely low recruitment percentages, as demonstrated for other Mediterranean plants growing in similar habitats (Sulis et al. 2018; Pisanu et al. 2012; Cogoni et al. 2019).

4.1 Implication for conservation

Our results provide useful information both at the habitat and species level to enhance the conservation status of this isolated population. In particular, it is essential primarily to conserve the phrygana habitat where the species grows, being the continuous decline in habitat quality among the main threats for this species. Moreover, we found that the isolated population of *S. thymbra* is unable per se to maintain in the future being its recruitment percentages extremely low to guarantee that new individuals can increase the size of the population; in such context of seedling emergence and recruitment irrelevant for the long-term population persistence, conservation actions can be focused to strictly protect and, if possible, enhance the number of adult plants, which is the key element to increase the population growth rate. Specifically, to increase the population size we suggest to carry out a specific translocation program for the unique Sardinian population located in San Michele hill. Indeed, as previously demonstrated for other plants (Cogoni et al. 2012; Mendoza et al. 2009), the emergence and establishment of seedlings are both the most critical phases in the life cycle of this plant. Therefore, a reintroduction project could be carried out to reinforce the population of *S. thymbra* using juvenile plants ex situ multiplied as previously done for other threatened Mediterranean plants (Fenu et al. 2019). Additionally, considering the increasing of climate change effects, it would be considered the possibility to test the use of specific management tools, such as watering the station of *S. thymbra* in case of long-lasting drought periods and, as suggested by de Villalobos et al. (2002), it would be advisable to use the practice controlled burning, also known as prescribed burning, which could result in preventing spread fires, and, contemporaneously, in the containment of existing vegetation, hence probably in the increasing of germination percentages of seeds. Finally, a sensibilization campaign aimed to raise the awareness of the public and institution may be the right strategy for plant conservation in this specific natural context.

This study highlighted the extreme complexity of the process mediated by germination patterns in the field, the seedling establishment, the importance of facilitative processes, the direct and indirect effects of human activities in the evolutionary dynamics in natural communities, and their

212

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

interaction with endangered plants. A full comprehension of natural processes is required to be able to properly manage natural habitats and substantially improve our ability to conserve several isolated small populations growing in highly sensitive impacted areas like those located near and/or within urban contexts. Finally, our findings increased the knowledge of the effect of habitat and time emergence in the recruitment pattern of the small isolated population of *S. thymbra*, although further research about the recruitment pattern, specifical stages from seed to seedling, is needed to deepen our knowledge and improve management and conservation efforts.

Compliance with ethical standards

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Andivia E, Villar-Salvador P, Tovar L, Rabasa S, Rey Benayas JM (2017) Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond. J Veg Sci 28:639–648. https://doi.org/10.1111/jvs.12520

Ballantyne M, Pickering CM (2015) The impacts of trail infrastructure on vegetation and soils: current literature and future directions. J Environ Manag 164:53–64. https://doi.org/10.1016/j.jenvman.2015.08.032

Biondi E, Mossa L (1992) Studio fitosociologico del promontorio di Capo S. Elia e dei colli di Cagliari (Sardegna). Doc Phytosoc 14:1–44

Bocchieri E, Fogu MC, Bacchetta G, Mossa L (2000) Le piante rare e/o in pericolo di estinzione della provincia di Cagliari e la strategia dell'Orto Botanico per la conservazione della biodiversità. Boll Soc Sarda Sci Nat 32:157–167

Bond WJ, Honig M, Maze KE (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. Oecologia 120:132–136

Bryant MM (2006) Urban landscape conservation and the role of ecological greenways at local and metropolitan scales. Landsc Urban Plan 76:23–44. https://doi.org/10.1016/j.landurbplan.2004.09.029

Callaway RM (1995) Positive interactions among plants. Bot Rev 61:306–349

Castilla AR, Alonso C, Herrera CM (2011) Exploring local borders of distribution in the shrub *Daphne laureola*: individual and population traits. Acta Oecol 37:269–276. https://doi.org/10.1016/j.actao.2011.02.011

Çatav ŞS, Bekar I, Ateş BS, Ergan G, Oymak F, Ülker ED et al (2012) Germination response of five eastern Mediterranean woody species to smoke solutions derived from various plants. Turk J Bot 36:480–487. https://doi.org/10.3906/bot-1111-12

Çatav ŞS, Küçükakyüz K, Akbaş K, Tavşanoğlu Ç (2014) Smoke-enhanced seed germination in Mediterranean Lamiaceae. Seed Sci Res 24:257–264. https://doi.org/10.1017/S0960258514000142

Çatav ŞS, Küçükakyüz K, Tavşanoğlu Ç, Pausas JG (2018) Effect of fire-derived chemicals on germination and seedling growth in Mediterranean plant species. Basic Appl Ecol 30:65–75. https://doi.org/10.1016/j.baae.2018.05.005

Cerabolini B, Ceriani RM, Caccianiga M, De Andreis R, Raimondi B (2003) Seed size, shape and persistence in soil: a test on Italian flora from Alps to Mediterranean coasts. Seed Sci Res 13:75–85. https://doi.org/10.1079/SSR2002126

Cogoni D, Mattana E, Fenu G, Bacchetta G (2012) From seed to seedling: a critical transitional stage for the Mediterranean psammophilous species *Dianthus morisianus* (Caryophyllaceae). Plant Biosyst 146:910–917. https://doi.org/10.1080/11263504.2011.647106

Cogoni D, Fenu G, Bacchetta G (2013) Effects of timing of emergence and microhabitat conditions on the seedling performance of a coastal Mediterranean plant. Ecoscience 20:131–136. https://doi.org/10.2980/20-2-3583

Cogoni D, Sulis E, Bacchetta G, Fenu G (2019) The unpredictable fate of the single population of a threatened narrow endemic Mediterranean plant. Biodivers Conserv 28:1799–1813. https://doi.org/10.1007/s10531-019-01757-0

de Villalobos AE, Pelaez DV, Boo RM, Mayor MD, Elia OR (2002) Effect of high temperatures on seed germination of *Prosopis caldenia* Burk. J Arid Environ 52:371–378. https://doi.org/10.1006/jare.2002.1004

Dell'Agli M, Sanna C, Rubiolo P, Basilico N, Colombo E, Scaltrito MM et al (2012) Anti-plasmodial and insecticidal activities of the essential oils of aromatic plants growing in the Mediterranean area. Malar J 11:219. https://doi.org/10.1186/1475-2875-11-219

Euro+Med PlantBase (2020) The information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/. Accessed 27 Jan 2020

Fenu G, Cogoni D, Navarro FB, Concas E, Bacchetta G (2017) The importance of the *Cisto-Lavanduletalia* coastal habitat on population persistence of the narrow endemic *Dianthus morisianus* (Caryophyllaceae). Plant Spec Biol 32:156–168. https://doi.org/10.1111/1442-1984.12138

Fenu G, Bacchetta G, Charalambos SC, Fournaraki C, Giusso del Galdo GP, Gotsiou P et al (2019) An early evaluation of translocation actions for endangered plant species on Mediterranean islands. Plant Divers 41:94–104. https://doi.org/10.1016/j.pld.2019.03.001

Gargano D, Fenu G, Medagli P, Sciandrello S, Bernardo L (2007) The status of *Sarcopoterium spinosum* (Rosaceae) at the western periphery of its range: ecological constraints lead to conservation concerns. Isr J Plant Sci 55:1–13

Géhu JM (1986) Des complexes de groupements végétaux à la phytosociologie paysagère contemporaine. Ital Bot [Inform Bot Ital] 18:53–83

Giménez-Benavides L, Escudero A, Iriondo JM (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. Ann Bot 99:723–734. https://doi.org/10.1093/aob/mcm007

Golan S, Waitz Y, Ziffer-Berger J, Barzilai M, Hanin N, Henkin Z et al (2019) Germination behavior of *Sarcopoterium spinosum* in response to smoke chemicals indicates adaptation to fire in the south-eastern Mediterranean. Isr J Plant Sci 66:103–111. https://doi.org/10.1163/22238980-00001069

Gómez JM, Hódar JA, Zamora R, Castro J, García D (2001) Ungulate damage on Scots pines in Mediterranean environments: effects of association with shrubs. Can J Bot 79:739–746. https://doi.org/10.1139/b01-055

Gómez-Aparicio L, Valladares F, Zamora R, Quero JL (2005) Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28:757–768. https://doi.org/10.1111/j.2005.0906-7590.04337.x

Rendiconti Lincei. Scienze Fisiche e Naturali (2021) 32:205–213

213

Gulias J, Traveset A, Riera N, Mus M (2004) Critical stages in the recruitment process of *Rhamnus alaternus* L. Ann Bot Lond 93:723–731. https://doi.org/10.1093/aob/mch100

He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett 16:695–706. https://doi.org/10.1111/ele.12080

Herranz JM, Ferrandis P, Martínez-Sánchez JJ (1998) Influence of heat on seed germination of seven Mediterranean Leguminosae species. Plant Ecol 136:95–103. https://doi.org/10.1023/A:1009702318641

Howell N (1981) The effect of seed size and relative emergence time on fitness in a natural population of *Impatiens capensis* Meerb. (Balsaminaceae). Am Midl Nat. https://doi.org/10.2307/2424749

Ibáñez I, Schupp EW (2001) Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. Oecologia 129:543–550. https://doi.org/10.1007/s004420100757

Itani M, Al Zein M, Nasralla N, Talhouk SN (2020) Biodiversity conservation in cities: defining habitat analogues for plant species of conservation interest. PLoS ONE 15:e0220355. https://doi.org/10.1371/journal.pone.0220355

Kadis C, Georghiou K (2010) Seed dispersal and germination behavior of three threatened endemic labiates of Cyprus. Plant Spec Biol 25:77–84. https://doi.org/10.1111/j.1442-1984.2009.00265.x

Keeley JE, Bond WJ (1997) Convergent seed germination in South African fynbos and Californian chaparral. Plant Ecol 133:153–167. https://doi.org/10.1023/A:1009748603202

Leck MA, Parker VT, Simpson RL (2008) Seedling ecology and evolution. Cambridge University Press, Cambridge

Martinoli G (1950) *Satureja thymbra* L., elemento Mediterraneo-Orientale della Sardegna. Ital Bot [Inform Bot Ital] 56:576–592. https://doi.org/10.1080/11263505009431488

Mendoza I, Zamora R, Castro J (2009) A seeding experiment for testing tree-community recruitment under variable environments: implications for forest regeneration and conservation in Mediterranean habitats. Biol Conserv 142:1491–1499. https://doi.org/10.1016/j.biocon.2009.02.018

Moles AT, Westoby M (2004) What do seedlings die from and what are the implications for evolution of seed size? Oikos 106:193–199

Moreira B, Pausas JG (2018) Shedding light through the smoke on the germination of Mediterranean Basin flora. S Afr J Bot 115:244–250. https://doi.org/10.1016/j.sajb.2016.10.008

Moreira B, Tormo J, Estrelles E, Pausas J (2010) Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Ann Bot Lond 105:627–635. https://doi.org/10.1093/aob/mcq017

Navarro-Cano JA, Verdú M, García C, Goberna M (2015) What nurse shrubs can do for barren soils: rapid productivity shifts associated with a 40 years ontogenetic gradient. Plant Soil 388:197–209. https://doi.org/10.1007/s11104-014-2323-2

Pickering CM, Hill W (2007) Impacts of recreation and tourism on plant biodiversity and vegetation in protected areas in Australia. J Environ Manag 85:791–800. https://doi.org/10.1016/j.jenvman.2006.11.021

Pickering CM, Hill W, Newsome D, Leung YF (2010) Comparing hiking, mountain biking and horse-riding impacts on vegetation and soils in Australia and the United States of America. J Environ Manag 91:551–562. https://doi.org/10.1016/j.jenvman.2009.09.025

Pignatti S, Guarino R, La Rosa M (2017) Flora d'Italia, vol 4, 2nd edn. Edagricole—Edizioni Agricole di New Business Media, Bologna

Pinna MS, Cañadas EM, Bacchetta G (2014) Initial constraints in seedling dynamics of *Juniperus macrocarpa* Sm. Plant Ecol 215:853–861. https://doi.org/10.1007/s11258-014-0337-8

Pinna MS, Fenu G, Cogoni D, Bacchetta G (2015) Schede per una lista rossa della flora vascolare e crittogamica italiana *Satureja thymbra* L. Ital Bot [Inform Bot Ital] 47:245–289

Pisanu S, Farris E, Filigheddu R, García MB (2012) Demographic effects of large, introduced herbivores on a long-lived endemic plant. Plant Ecol 213:1543–1553. https://doi.org/10.1007/s11258-012-0110-9

Pouget M, Youssef S, Migliore J, Juin M, Médail F, Baumel A (2013) Phylogeography sheds light on the central–marginal hypothesis in a Mediterranean narrow endemic plant. Ann Bot Lond 112:1409–1420. https://doi.org/10.1093/aob/mct183

Pugnaire FI, Armas C, Maestre FT (2011) Positive plant interactions in the Iberian Southeast: mechanisms, environmental gradients, and ecosystem function. J Arid Environ 75:1310–1320. https://doi.org/10.1016/j.jaridenv.2011.01.016

Quézel P, Médail F (2017) Ecologie et biogéographie des forêts du bassin Méditerranéen, Editions scientifiques. Elsevier, Paris

Rey PJ, Alcántara J (2000) Recruitment dynamics of a fleshy fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J Ecol 88:622–633. https://doi.org/10.1046/j.1365-2745.2000.00472.x

Schenk HJ, Mahall BE (2002) Positive and negative plant interactions contribute to north–south–patterned association between two desert shrub species. Oecologia 132:402–410. https://doi.org/10.1007/s00442-002-0990-9

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sulis E, Bacchetta G, Cogoni D, Fenu G (2017) Reproductive performance of *Helianthemum caput-felis* along its fragmented distribution in the Mediterranean coasts. Flora 234:24–33

Sulis E, Bacchetta G, Cogoni D, Fenu G (2018) Short-term population dynamics of *Helianthemum caput-felis*, a perennial Mediterranean coastal plant: a key element for an effective conservation program. Syst Biodivers 16:774–783. https://doi.org/10.1080/14772000.2018.1492469

Sulis E, Bacchetta G, Cogoni D, Gargano D, Fenu G (2020) Assessing the global conservation status of the rock rose *Helianthemum caput-felis*. Oryx 54:197–205. https://doi.org/10.1017/S0030605318001424

Thanos CA, Doussi MA (1995) Ecophysiology of seed germination in endemic labiates of Crete. Isr J Plant Sci 43:227–237

Thanos CA, Kadis CC, Skarou F (1995) Ecophysiology of germination in the aromatic plants thyme, savory and oregano (Labiatae). Seed Sci Res 5:161–170. https://doi.org/10.1017/S0960258500002786

Thompson JD (2005) Plant evolution in the Mediterranean. Oxford University Press, Oxford

Turkington R, Goldberg DE, Olsvig-Whittaker L, Dyer AR (2005) Effects of density on timing of emergence and its consequences for survival and growth in two communities of annual plants. J Arid Environ 61:377–396. https://doi.org/10.1016/j.jaridenv.2004.09.016

Weekley CW, Menges ES, Quintana-Ascencio PF (2007) Seedling emergence and survival of *Warea carteri* (Brassicaceae), an endangered annual herb of the Florida scrub. Can J Bot 85:621–628. https://doi.org/10.1139/B07-061

Widawski K, Jary Z (2019) Mass tourism in protected areas—underestimated threat? Polish National Parks case study. Open Geosci 11:1046–1060. https://doi.org/10.1515/geo-2019-0081

Yakimowski SB, Eckert CG (2007) Threatened peripheral populations in context: geographical variation in population frequency and size and sexual reproduction in a clonal woody shrub. Conserv Biol 21:811–822. https://doi.org/10.1111/j.1523-1739.2007.00684.x