The role of shrubs in spatially structuring the soil seed bank of perennial species in a semi-arid gypsum plant community.

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Abstract

The soil seed bank is crucial for the stability and regeneration of the specialised gypsum plant communities. The presence of shrubs influences the spatial structure of the soil seed bank by trapping more or fewer seeds depending on their physiognomic attributes or, for example, by providing seeds through the plants established under canopies. We aimed to unravel the potential role of different shrub species with diverse physiognomy in determining the spatial structure of the soil seed bank in a semi-arid gypsum plant community of NE Spain. We examined richness and abundance of the soil seed bank at different microsites associated with four dominant shrubs of different size-type (tall or short), and architecture (crawling-branched or erect). We found more considerable richness and abundance of seeds of perennial species within shrub canopies than in open areas. Specifically, the crawling-branched shrubs *Gypsophila struthium* and *Helianthemum squamatum*, and the tall erect shrub *Ononis tridentata* accumulated the most abundant soil seed banks of perennials, thus having an important structuring role. Conservation and restoration efforts should focus on gypsophyte shrubs (*G. struthium, O. tridentata* and *H. squamatum)*, which can enhance community stability and regeneration through the formation of an abundant soil seed bank of perennial species in gypsum plant communities.

Keywords: complete seed bank, gypsophytes, perennial species**,** seed sink, seed trapping.

Nomenclature: Castroviejo et al. (1986-2005)

Introduction

The soil seed bank is an essential component of plant communities since it constitutes a reservoir in the soil of viable propagules ready to germinate or in a dormant state (Csontos 2007). It promotes diversity in plant communities, acting as a temporary buffer against unfavourable conditions that decrease plant survival and seed production (Venable and Brown 1988). Thus, the soil seed bank contributes to community regeneration processes (Luzuriaga et al. 2005; Martínez-Duro et al. 2009; Martinez-Duro et al. 2012; Olano et al. 2012), being relevant for plant community stability through time (Mall and Singh 2014). In arid and semi-arid environments, where plants are submitted to high environmental stochasticity due to unpredictable water inputs (Noy-Meir 1973), the formation of a robust soil seed bank is crucial for plant community endurance (Luzuriaga et al. 2005; Olano et al. 2012). Specifically, semi-arid gypsum environments harbour rare species and specialised plant communities whose dynamics often rely on the formation of a robust seed bank (Caballero et al. 2003; Aragón et al. 2007). Therefore, a proper conservation and restoration management of gypsum ecosystems requires a better understanding of the processes shaping the soil seed bank in these plant communities (Martinez-Duro et al. 2012; Olano et al. 2012).

In arid and semi-arid plant communities, the typical island-like spatial distribution of shrubs (Maestre and Cortina 2005) influences the spatial distribution of the soil seed bank (Pugnaire and Lázaro 2000; Caballero *et al.* 2008a; López-Peralta *et al.* 2016). Shrubs can act as seed sinks by physically obstructing and accumulating seeds which are transported horizontally either by wind or water, when flowing speed decreases compared to open areas (Thiede and Augspurger 1996; Nathan et al. 2002; Bullock and Moy 2004; Aerts et al. 2006). The physiognomic attributes of shrubs may influence the seed trapping and accumulation by, for example, intercepting more wind-dispersal seeds as the taller the plant is and retaining more seeds as the denser and more crawling the branches are (Thiede and Augspurger 1996; Bullock and Moy 2004; Aerts et al. 2006). Moreover, the cumulative effect of shrubs can be reinforced by the physical protection of seeds from predators (Smit et al. 2008) and also because shrubs may be used as perches by birds that deposit seeds in the surroundings (Pausas et al. 2006). On the other hand, although some shrubs can inhibit the germination of some species (Foronda et al., 2018), they often harbour a high plant diversity under canopies (Foronda et al. 2019; Soliveres et al. 2011) by creating favourable microhabitats for plant establishment and protecting seedlings from grazing and trampling (Callaway 2007). These diversity patches can act as seed sources (Caballero *et al.* 2008a; Filazzola et al. 2019), accumulating a vast amount of seeds in the vicinity due to short-range seed dispersal typical in these communities (Olano et al. 2005; Martinez-Duro et al. 2012). Therefore, shrubs favour the formation of a particularly dense seed bank in their vicinity, showing a gradual decline from the shrub centre to the peripheral areas (Bullock and Moy 2004; Caballero *et al.* 2008a). However, our understanding of the role that diverse shrub species with different size and architecture have on the spatial patterning of the soil seed bank in gypsum plant communities is still limited.

Several studies have contributed to the understanding of the dynamics of the soil seed bank and the spatial relationships with the above-ground vegetation in gypsum plant communities (Caballero *et al.* 2003, 2005; Olano *et al.* 2005; Caballero *et al.* 2008b; López-Peralta *et al.* 2016). However, many of these studies are mainly focused on annuals-rich plant communities, whose persistence depends entirely on seed production (García and Zamora 2003), shaping robust but transient soil seed banks that generally germinate within a year of initial dispersal (Thompson 2000). Less is known about the spatial patterning of soil seed banks composed predominantly of perennials, whose population dynamics do not rely so strongly on seed production (García and Zamora 2003). Seeds of perennials can remain in a dormant state for more than one year thus shaping persistent soil seed banks (Thompson 2000; Leck 2012), likely spatially structured by secondary dispersal due to wind and water flow to a greater extent than transient seed banks (Nathan and Muller-Landau 2000).

This study aimed to unravel the potential role of different shrub species with diverse physiognomy in determining the spatial structure of the soil seed bank in a semi-arid gypsum plant community of NE Spain. To do so, we sampled the complete and the persistent soil seed bank from the centre to nearby open areas of four dominant shrub species in the community, with contrasting size-type (tall *versus* short) and architecture (crawling-branched *versus* erect). We hypothesised that richness and abundance of the soil seed bank would be higher under shrub canopies than in open areas because of a strong cumulative effect of shrubs.. Specifically, we expected to find the highest richness and abundance of seeds associated with tall shrubs with crawling-branched architecture because they may be better able to intercept wind-dispersal seeds and retain them through crawling branches (Bullock and Moy 2004). . Moreover, given that plants harboured in vegetation patches would shed seeds to the local vicinity thus acting as seed sources (Filazzola et al. 2019), shrubs with a strong nurse role in the community (Foronda *et al.* 2019) were supposed to shape the richest and most abundant soil seed banks.

Materials and methods

Study area

We conducted the study in the Middle Ebro Valley (NE Spain), which encompasses one of the most massive gypsum outcrops in Europe (Machín and Navas 1998). The lithology in this area is mainly gypsum alternating with marls, limestones, and clays (Quirantes 1978). This area has a semi-arid Mediterranean climate with strong continental influence (Creus and Ferraz 1995). The landscape is characterised by low hills and flat-bottomed areas with traditional agro-pastoral use, consisting mainly of cereal crops and extensive sheep livestock (Pueyo and Alados 2007).

Specifically, we performed the study in “La Lomaza de Belchite” Wildlife Reserve (41º23’33” N 0º42’18” W, 410 m a.s.l.), which consists of a low gypsum hill protected from agro-pastoral activities. The average annual temperature in the study site is 14.7 ºC, and average annual precipitation is 302 $mm \cdot yr^{-1}$, with the main rainfall events occurring in May and November (“Z02 Belchite” meteorological station; 2004-2019 period; SIAR-Ministerio de Agricultura, Pesca, Alimentación y Medio Ambiente; http://www.siar.es). Plant community in the study site consists of a patchy scrubland-grassland with a predominance of shrubs, subshrubs, and perennial grasses, together with annual forbs and annual grasses (Table S1). Many of the species are substrate-specialists (i.e., gypsophytes) as *Gypsophila struthium* Loefl. subsp. *hispanica* (Willk.) G. López, *Ononis tridentata* L., *Helianthemum squamatum* (L.) Pers. and *Herniaria fruticosa* L. (Mota et al. 2011).

Target species

We selected as target species two of the most abundant tall shrubs and two of the most abundant short shrubs in the plant community in the study area, which accounted for a relative abundance of 45 % among shrubs in the study site (Table S2). We selected one species with crawling-branched architecture and one species with erect architecture per size-type (i.e., tall or short; Fig. 1). Target species were a) *Gypsophila struthium* Loefl. subsp. *hispanica* (Willk.) G. López (CARYOPHYLLACEAE), a 47 ± 3 cm tall gypsophilous crawling-branched nanophanerophyte; b) *Ononis tridentata* L. (FABACEAE), a 53 ± 2 cm tall gypsophilous erect nanophanerophyte; c) *Helianthemum squamatum* (L.) Pers. (CISTACEAE), a 21 ± 1 cm tall gypsophilous crawling-branched chamaephyte and d) *Thymus vulgaris* L. (LAMIACEAE), a 25 ± 1 cm tall non-gypsophilous erect chamaephyte (Fig. 1 and Table S3).

Soil seed bank survey

We collected soil cores in three microsites from the centre to peripheral areas of 25 random individuals per target species coexisting interspersed in the same location (an area of less than 0.5 Km^2) and separated at least one meter from each other to avoid interdependence (Fig. S1). Microsites were a) under the shrub canopy, almost in the centre of the shrub (under); b) at the edge of the shrub, whose width was considered the 10% of the canopy radius (edge); and c) open areas not covered by perennial plants, in the potential area of influence of the shrub, 30-50 cm away from the edge of the target species depending on the shrub size (open). We vertically collected 10 cm deep soil cores (3.5 cm diameter), considered a sufficient depth for sampling the entire seed bank in drylands (Guo et al. 1998). We collected soil samples in winter (February 2015), after the autumn germination peak typical in gypsum communities (Escudero et al. 1997), to quantify the persistent seed bank, and in late summer (September 2015), after seeds shedding, to quantify the complete soil seed bank (Caballero et al. 2005). Samples were collected in the prevailing windward direction (W-NW) to account for wind-dispersal seeds (Bullock and Moy 2004). We measured the height (m) of the target species in each of the 25 individuals in both sampling periods.

To quantify seeds in the soil samples (n = 600 samples = 4 target species x 25 individuals x 3 microsites x 2 sampling periods), we used the seedling emergence method (Heerdt et al. 1996), which enables the identification of only viable seeds (active seed bank; Csontos 2007). Soil samples were kept in airtight plastic bags and stored in a cold chamber at 4°C until we set them in a greenhouse for seeds germination (March 2015 and March 2016 for winter and summer samples respectively). We first soaked the soil samples for ten minutes in a $NaHCO_3$ solution (70 $g \cdot l^{-1}$) for clay disaggregation, and then washed and sieved them over a 4 mm mesh to remove the coarse fraction of the soil and pieces of roots, branches or leaves. To obtain seed-rich samples, we re-sieved samples over a 0.25 mm mesh, which was small enough to retain seeds of all species living in the community (Table S1). Sieving may produce seeds scarification, favouring the germination of hard-coated seeds (Albert et al. 2002; Pérez-García and González-Benito 2006). We arranged the resulting samples in 23 × 9 × 7 cm trays, using one tray per soil core. We filled the trays with a commercial substrate (70% white peat and 30% pine forest soil) to provide support for the emerged seedlings. To prevent the emergence of potential germinated seeds from the substrate, we laid the samples on a 0.25 mesh nylon cloth placed on top of the substrate. Then, we set the trays in the greenhouse (Estación Experimental Aula Dei-CSIC, Zaragoza: 41º43'31"N 0º48'43"W) under controlled temperature regimes (25°C during the day and 15°C during the night) and natural lightning (12-15 daylight hours).

We monitored seedling emergence once a week for 20 weeks (from March to July) to quantify species richness (number of species) and seed abundance (number of seedlings) at each sample. As soon as we identified an emerged seedling to the species level, it was removed from the tray. When identification at species level was not feasible after two weeks of being emerged, seedlings were transplanted into individual pots and allowed to grow. We watered the trays three times a week with fresh water, simulating a soft rain with a showerhead to avoid seedling damage. After 12 weeks, we irrigated the trays once a week for four weeks with a gibberellic acid solution (1 $g \cdot l^{-1}$ GA_3, GIBERLUQ-L) to induce germination of physiologically dormant seeds (Albert et al. 2002). We then monitored seedling emergence until the end of the assay, but germination hardly occurred (< 5 % of the total emerged seedlings were recorded after 12 weeks; Fig. S2).

Data analyses

For the complete and the persistent seed bank separately, we tested significant effects of the microsite ('under', 'edge' and 'open') and the target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) on richness and abundance of both annuals and perennials emerged by fitting Generalised Linear Models (GLMs). Plant height (m) was included as a covariate. GLMs were fitted with Poisson error distribution and log link function because count data did not meet the assumptions of normality. When we found significant effects, we applied Tukey's post-hoc multiple comparisons to detect significant differences among microsites and among target species. Seeds from the target species recorded in microsites linked to conspecific shrubs were excluded from the analyses because the donation of seeds by parental plants was not an objective of this study.

We performed all statistical analyses in R software, using the packages 'stats' (GLMs for differences in richness and abundance; R Core Team 2017) and 'multcomp' (multiple comparisons after GLMs; Hothorn et al. 2008).

Results

A total of 685 seedlings belonging to 13 taxa emerged from the persistent soil seed bank, and a total of 1,784 seedlings belonging to 28 taxa emerged from the complete soil seed bank. Soil seed bank was mainly formed by perennials, with 69 % of the richness and 94% of the abundance in the persistent seed bank and 61 % of the richness and 86% of the abundance in the complete seed bank (Table 1). The gypsophyte *H. fruticosa* was the most representative perennial species in both the persistent and the complete seed bank, followed by *H. squamatum* (Table 1). We discarded annuals from the following analyses due to potential underestimation (only the 33% of the annual species previously found in above-ground vegetation surveys occurred in the soil seed bank samples; Table 1 and Table S.1), likely because some of them could have undergone high mortality rate due to the cold-wet conditions at storage (Marcos Filho 2015). Besides, since the species found in the persistent soil seed bank were a subset of the species found in the complete soil seed bank (Table 1), only results of the complete soil seed bank are presented in detail. But see results for annuals and the persistent seed bank in Tables S4-S6 and Figures S3-S13 in Supplementary material.

We found significant effects of the microsite in the richness of perennials in the complete soil seed bank (Table 2), being larger in 'under' microsite than in the other microsites, and being also larger at 'edge' microsite than in 'open' microsite (Fig. 2). However, no effect of the target species was found in richness of perennials (Table 2). Plant height was positively correlated to the richness of perennials, with low values of Pearson's r (Table 2; Fig. 3).

We observed significant effects of the microsite and the target species in the abundance of perennials, with significant interactions between both independent variables (Table 2). Abundance was the largest in 'under' microsite linked to *O. tridentata*, followed by *G. struthium* and *H. squamatum* (Fig. 4). Lower abundance of perennials was found in 'edge' microsite, where *H. squamatum* accumulated more seeds than the other shrubs (Fig. 4). Abundance of perennials was significantly larger in 'open' microsites associated with *G. struthium* than in those associated with the other target species (Fig. 4). Abundance of perennials was significantly larger when plants were taller in 'under' microsite, but not in 'edge' and 'open' microsites, but with low values of Pearson's r (Fig. 5).

Discussion

In line with previous studies carried out in semi-arid gypsum plant communities, our results highlight the role of shrubs as important elements in the community by spatially structuring the soil seed bank (Caballero *et al.* 2008a; López-Peralta *et al.* 2016). As we expected, soil seed bank richness and abundance were larger in microsites within the shrub canopy than in open areas. Moreover, we found a gradient in seed accumulation from the edge to the centre of shrubs, likely because of wind or water-mediated secondary transportation of seeds from the peripheral to the inner parts of shrubs (Aerts et al. 2006). Internal branches would act as substantial barriers to wind and water flows (Bullock and Moy 2004; Aerts et al. 2006), thus stopping and accumulating seeds in the centre of the shrubs. Redistribution of seeds towards the centre of shrubs seemed to be remarkable for perennials, and even it was notably observed in the persistent soil seed bank (Table S 4; Fig. S3). This can be owed to the force of time because the longer the seeds are exposed, the more subjected to secondary dispersion they are (Nathan and Muller-Landau 2000). This could explain the different findings in studies focused on annuals-rich communities, which did not observe significant differences between the edge and central locations of vegetation patches (Caballero *et al.* 2008a).

Our main finding was the differential roles of different shrub species with different physiognomy on spatially structuring the soil seed bank. While some of the studied shrub species accumulated a vast seed bank under their canopies (*i.e., G. struthium, O.*

tridentata and *H. squamatum*), other shrub species did not have such a substantial effect on the spatial structure of the soil seed bank (*i.e., T. vulgaris*). Consistent with other studies, we found that shrub height may influence the accumulation of seeds (Caballero *et al.* 2008a). Although as the taller was the shrub, the richer was the seed bank it formed under the canopy, this effect seemed to be weak. Nonetheless, our results suggested a species-specific influence on the accumulation of seeds that may be driven by the architecture of the shrub as well. In general, we observed that the crawling-branched shrubs (*e.g.*, *G. struthium*) were more able to aggregate seeds than the erect ones, and this fact seem to be especially observed for the annuals found in our experiment (Fig. S.8B and Fig. S.9). But the effect of shrubs on the accumulation of annual species should be tested with more caution in future studies. The better ability of crawling-branched shrubs may be due to the placement of branches that drag in the soil surface acting as physical barriers to seed distribution by runoff (Aerts et al. 2006).

Shrubs can accumulate seeds coming from other vegetation patches, but also seeds produced by plants co-occurring in their same patch, acting as both seed sinks and seed sources (Soriano et al. 1994). Plants in semi-arid gypsum areas typically show short-range dispersal (Olano et al. 2005; Martinez-Duro et al. 2012), thus accumulating their seeds in the local vicinity of parent plants. The shrubs harboring more plants underneath would then contribute to the formation of patches with abundant soil seed banks. Indeed, we observed that shrubs with a nurse role in our study site (*e.g.*, *G. struthium* and *O. tridentata*; Foronda et al. 2019) accumulated more seeds underneath. In our study site, the cumulative effect of *G. struthium* extended to the surrounding open areas, containing more seeds of perennials than open areas associated to the other shrubs, likely by a seed source effect (Caballero *et al.* 2008a). Given that seeds would contribute to above-ground vegetation and *viceversa* (Caballero et al. 2008b), complementary studies on similarities in species composition between both community compartments may give information about the provenance of seeds accumulated under the shrubs and in the surroundings. In our study system, we found that species composition of the soil seed bank and the above-ground vegetation harbored under the canopy of *G. struthium* and *O. tridentata* (nurse plants) are highly similar (Table S.7 and Fig. S.14). However, other mechanisms like seed dormancy or seed mortality can be acting (Adondakis and Venable 2004; Parsons 2012), thus modifying the species composition in the experiment. Further experiments focused on the mechanisms that can influence similarities in species composition are necessary to make strong conclusions about the seed source effect of shrubs.

This study revealed that size-type and architecture of shrubs have a role in the creation of species-rich islands, being in particular tall shrubs and shrubs with crawling-branched architecture, such as *G. struthium*, the ones that contribute the most to soil seed bank structure. Nevertheless, despite the seed accumulation driven by shrubs, a successful seedling establishment from the seed bank is not ensured. Instead, seedling establishment depends on the proper role of the shrub as a nurse plant because the seed bank would encounter suitable conditions for seeds germination (Callaway 2007). Therefore, identifying shrubs acting not only as seed accumulators but also as nurse plants would be valuable for plant community conservation and restoration efforts. Previous studies proved the facilitative role of *G. struthium* on a wide array of plant species leading to diverse and abundant understory vegetation (Navarro-Cano et al. 2016; Foronda et al., 2019).

In Mediterranean gypsum plant communities, the soil seed bank in late summer (i.e., complete seed bank) is supposed to parallel the above-ground vegetation in the growing season (Olano *et al.* 2005; Caballero *et al.* 2008b). Transient soil seed banks are primarily composed of annuals (Leck 2012) because their persistence in the community often relies on seed production (García and Zamora 2003). Differently to the assertion that soil seed banks in semi-arid gypsum environments are primarily composed of annuals and short-lived perennial species (Olano et al. 2012; Leck 2012), we predominantly recorded seeds of perennial species in both the complete and the persistent soil seed bank. This fact may be explained by the dominance of perennial plants in the community (Table S.1). Seeds of perennials would shape persistent soil seed banks, remaining in a dormant state for more than one year (Thompson 2000; Leck 2012). Indeed, the persistent soil seed bank in our study site was mainly composed of perennials of which the gypsophytes *H. fruticosa* and *H. squamatum* were dominant (the latter is known to be a short-lived perennial; de la Cruz et al. 2008). This fact supports the studies that argue that gypsum plants maintain a persistent soil seed bank (Caballero et al. 2003). Nevertheless, detailed spatiotemporal studies would be necessary to understand this finding fully.

In conclusion, this study contributed to the understanding of the role that dominant shrub species in the community have in spatially structuring the soil seed bank in semi-arid gypsum plant communities. The shrub species that most contributed to the formation of an abundant soil seed bank of perennials in gypsum plant communities of the Middle Ebro Valley were *G. struthium*, *O. tridentata* and *H. squamatum*. Thus, conservation and restoration efforts on these species are recommended, as they would enhance the stability and regeneration of these rare and specialised plant communities.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

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Figure captions

Fig. 1 Target species: A) *Gypsophila struthium* Loefl. subsp. *hispanica* (Willk.) G. López; B) *Ononis tridentata* L.; C) *Helianthemum squamatum* (L.) Pers.; and D) *Thymus vulgaris* L.

Fig. 2 Mean richness (number of species per m^2) of perennials found at each microsite in the complete soil seed bank. Different letters indicate significant differences between microsites after Tukey's multiple comparisons ($p \leq 0.05$).

Fig. 3 Correlations between richness of perennials (number of species per m^2) and the plant height (m) in all microsites and target species altogether in the complete soil seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

Fig. 4 Mean abundance (number of emerged seedlings per m^2) of perennials in different target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) per microsite (under the shrub canopy, at the edge of the shrub, and open areas) in the complete soil seed bank. Different letters indicate significant differences among target species after Tukey's multiple comparisons for each microsite separately.

Fig. 5 Correlations between abundance of perennials (number of emerged seedlings per m^2) and the plant height (m) per microsite in the complete seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

Table 1 Total density (individuals/m^2) of annual and perennial species recorded in the persistent and the complete soil seed banks.

	Persistent	Complete
Annuals		
Asterolinon linum-stellatum (L.) Duby	-	20.79
Bromus rubens L.	-	3.46
Campanula fastigiata Dufour ex A. DC	-	3.46
Cerastium pumilum Curtis	-	3.46
Chaenorrhinum rubrifolium (Robill. & Castagne ex DC.) Fourr.	110.87	675.60
Clypeola jonthlaspi L.	-	3.46
Filago pyramidata L.	20.79	83.15
Galium verrucosum Huds.	-	13.86
Linum strictum L.	6.93	20.79
Reseda stricta Pers.	-	10.39
Unknown annual	6.93	3.46
Perennials		
Brachypodium retusum (Pers.) P. Beauv.	-	24.25
Gypsophila struthium Loefl. subsp. *hispanica* (Willk.) G.López	3.46	41.58
Helianthemum squamatum (L.) Pers.	169.77	388.03
Helianthemum syriacum (Jacq.) Dum. Cours	-	72.76
Helichrysum stoechas (L.) Moench	62.36	377.64
Herniaria fruticosa L.	1863.95	3835.31
Koeleria vallesiana (Honck.) Gaudin	-	17.32
Launaea lanifera Pau	-	24.25
Linum suffruticosum L.	-	27.72
Moricandia arvensis (L.) DC.	-	3.46
Plantago albicans L.	27.72	69.29
Sedum sediforme (Jacq.) Pau	-	10.39
Sideritis hirsuta L.	-	6.93
Sonchus tenerrimus L.	6.93	34.65
Stipa sp.	20.79	79.69
Teucrium capitatum L.	24.25	17.32
Thymus sp.	48.50	308.35

Stipa sp. can be either *Stipa lagascae* Roem. & Schult. or *Stipa parviflora* Desf.; and *Thymus sp.* can be either *Thymus vulgaris* L. or *Thymus zygis* L. (difficult to identify at the seedling stage).

Table 2 Results of GLMs to test the effect of the microsite, the target species and the plant height, and the interaction among variables on soil seed bank richness and abundance of perennials emerged in the complete soil seed bank. Significant effects ($p \leq 0.05$) are highlighted in bold.

Dependent variables	**Explanatory variables**	**DF**	**Deviance**	**p-value**
Richness	Microsite	2	187.05	**<0.001**
	Target species	3	0.52	0.916
	Plant height	1	8.75	**<0.01**
	Microsite : Target species	6	8.86	0.181
	Microsite : Plant height	2	0.60	0.742
	Target species : Plant height	3	0.28	0.964
	Microsite : Target species : Plant height	6	2.61	0.856
Abundance	Microsite	2	1221.44	**<0.001**
	Target species	3	46.28	**<0.001**
	Plant height	1	37.42	**<0.001**
	Microsite : Target species	6	53.01	**<0.001**
	Microsite : Plant height	2	6.37	**<0.05**
	Target species : Plant height	3	5.20	0.158
	Microsite : Target species : Plant height	6	6.33	0.388

Figure 1

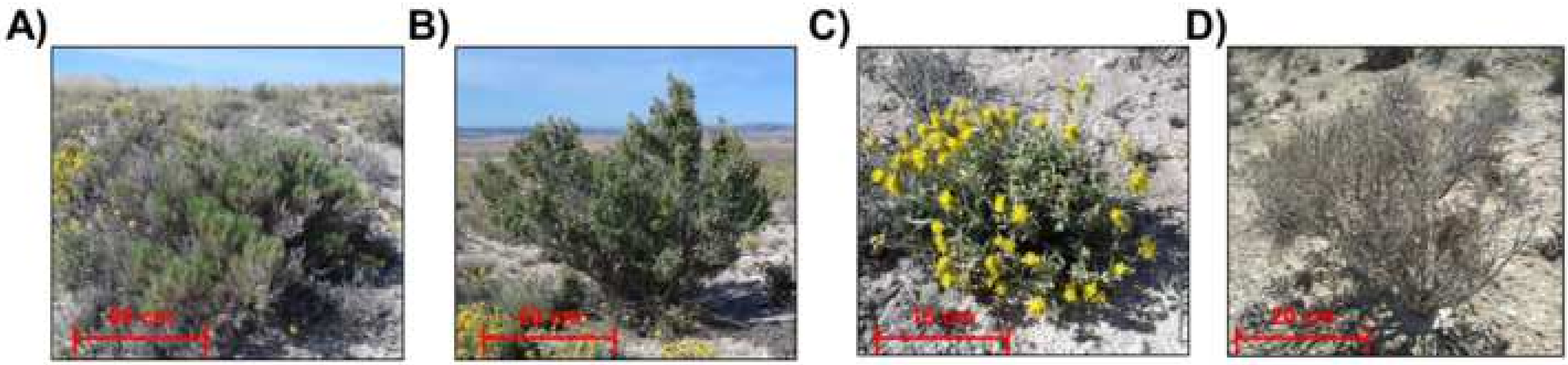

Figure 3 Click here to download Figure Fig 3_Correlation richness-height.tiff

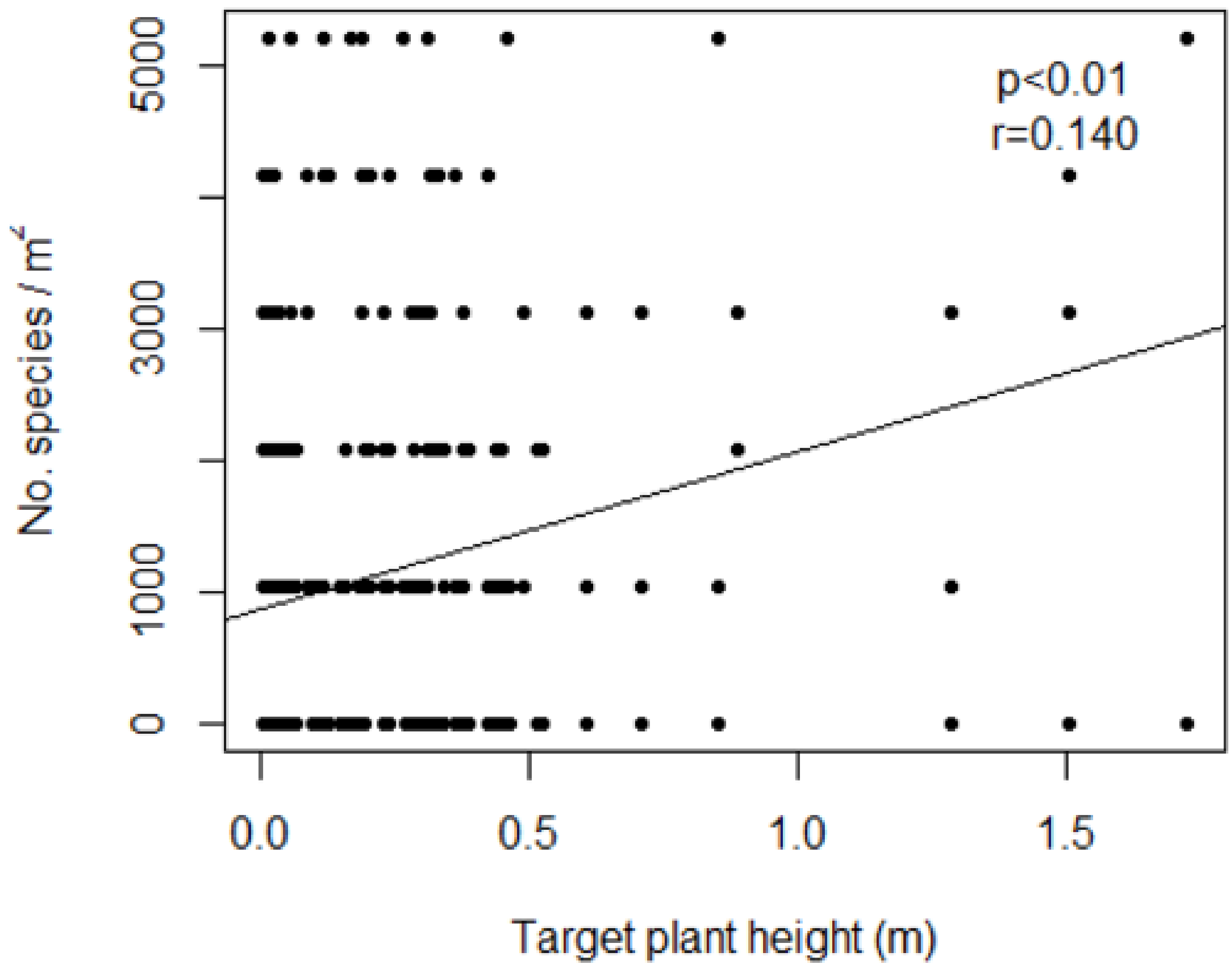

Figure 4

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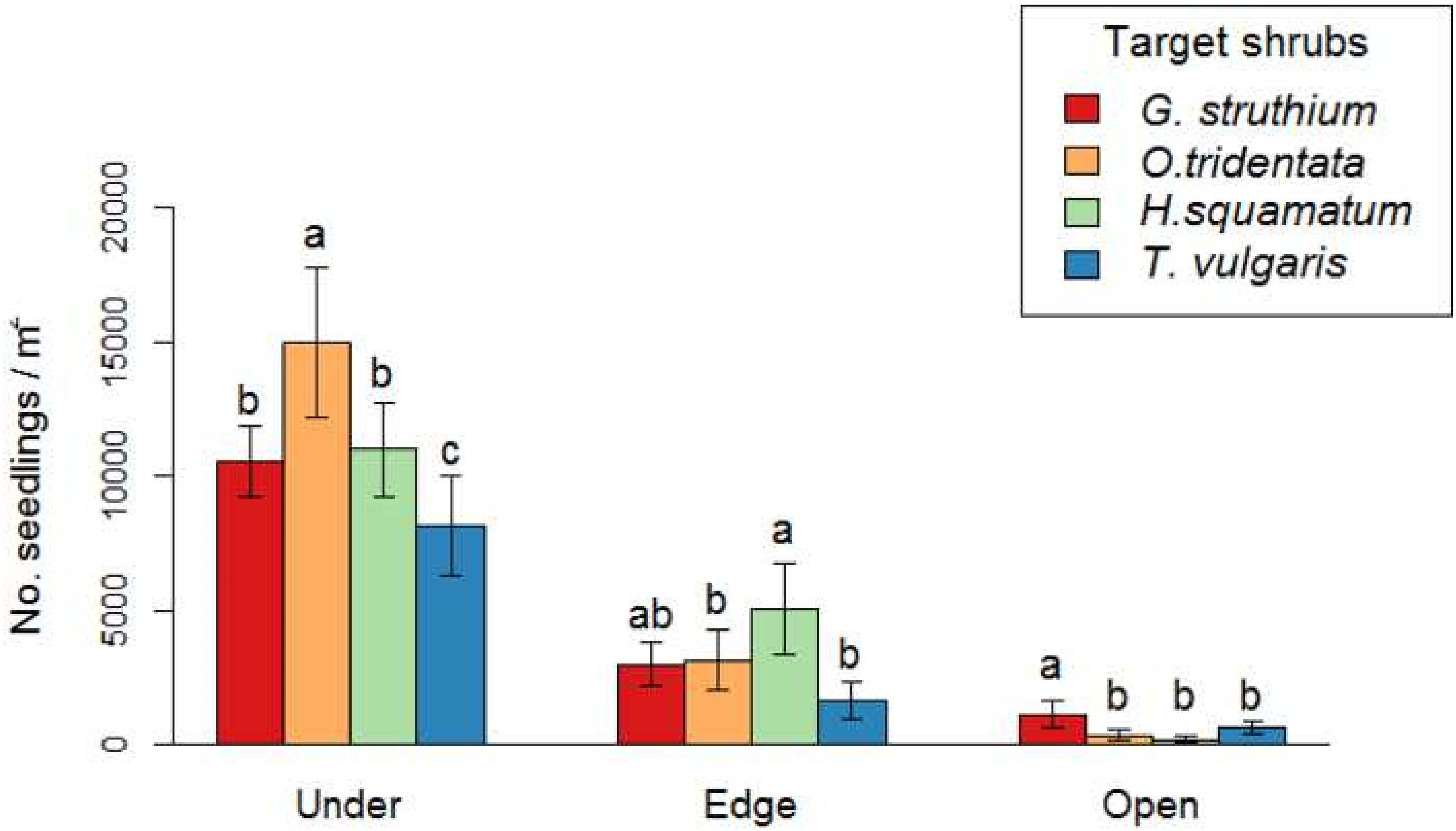


Figure 5

Click here to download Figure Fig 5_Correlation abund-height.tiff

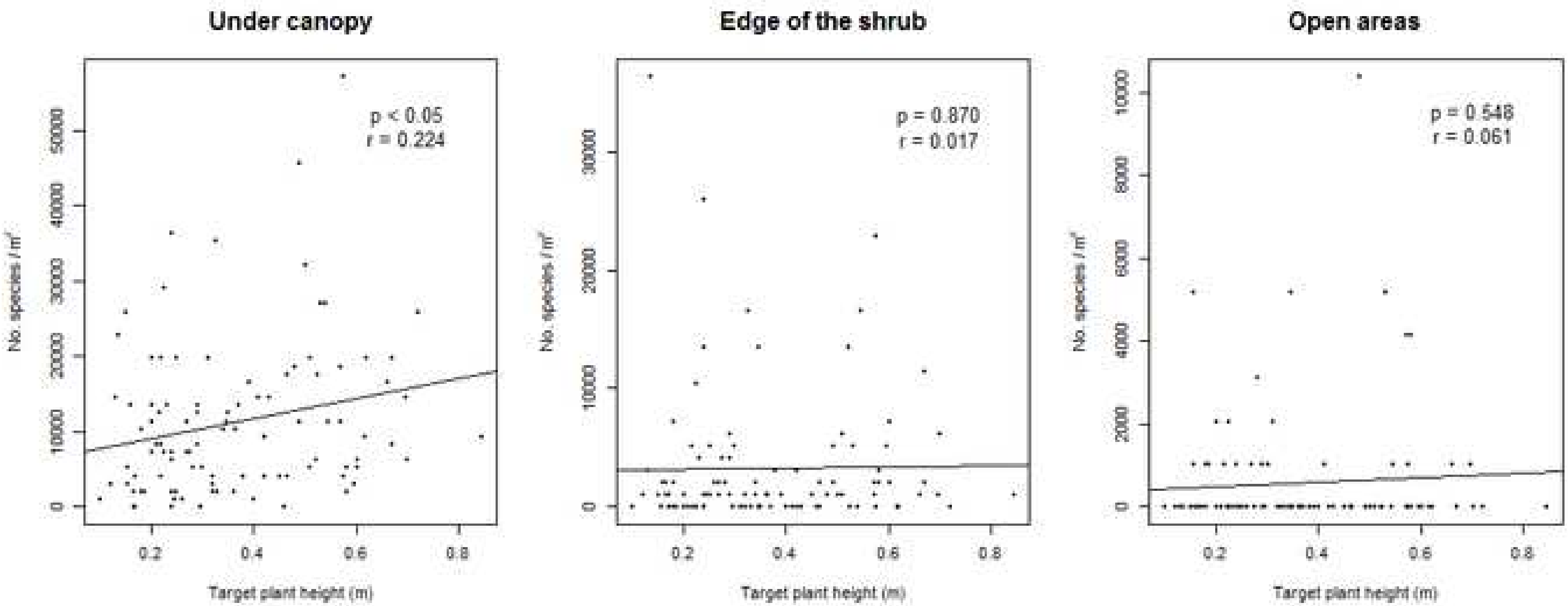
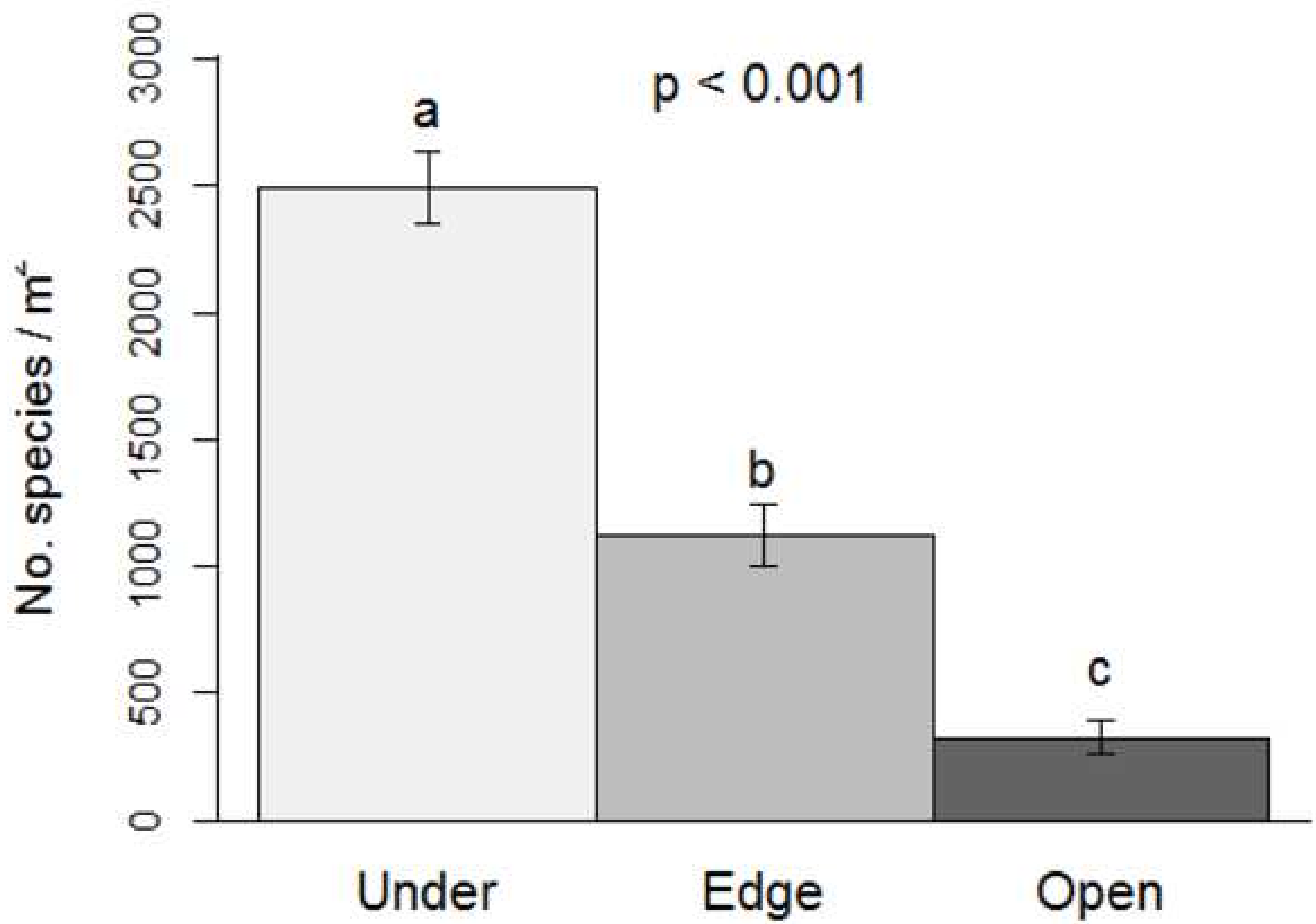


Figure 2



No. species / m²
0
500
1000
1500
2000
2500
3000
p < 0.001
a
b
c
Under
Edge
Open

Supplementary Information

Implications of shrubs for the spatial structure of the soil seed bank in a semi-arid gypsum plant community.

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<u>Appendix 1</u>. Characteristics of the plant community in the study site

Table S.1 Annual and perennial species in the study site: height, seed size and total density of individuals per species.

	Species	Family	Growth habit	Gypsophily	Plant height (cm)	Seed size (mm)	Total density (individuals/m^2)
	Annuals						
1	*Aegilops geniculata* Roth.	*Poaceae*	Graminoid	Gypsovag	15-40	7 x 3	0.05
2	*Alyssum alyssoides* (L.) L.	*Brassicaceae*	Forb	Gypsovag	5-15-30)	3-4 x 3-4	0.02
3	*Anagallis arvensis* L.	*Primulaceae*	Forb	Gypsovag	(2.5)8-40(70)	0.9-1.4 x 0.6-1	0.02
4	*Asterolinon linum-stellatum* (L.) Duby	*Primulaceae*	Forb	Gypsovag	(1)3 - 12-18)	1.2	18.75
5	*Brachypodium distachyon* (L.) P. Beauv.	*Poaceae*	Graminoid	Gypsovag	< 30	1-2 x 3-4	0.99
6	*Bromus rubens* L.	*Poaceae*	Graminoid	Gypsovag	< 60	NA	1.93
7	*Bupleurum semicompositum* L.	*Umbelliferae*	Forb	Gypsovag	2 - 35	1-1.5 x 0.4-0.7	0.11
8	*Campanula fastigiata* Dufour ex A. DC	*Campanulaceae*	Forb	Gypsophyte	3.5-6	0.35 x 0.2-0.3	NA
9	*Cerastium pumilum* Curtis	*Caryophyllaceae*	Forb	Gypsovag	10	0.5 x 0.5	0.11
10	*Chaenorrhinum rubrifolium* (Robill. & Castagne ex DC.) Fourr.	*Scrophulariaceae*	Forb	Gypsovag	5-18	0.3-0.5 x 0.25-0.3	8.27
11	*Clypeola jonthlaspi* L.	*Brassicaceae*	Forb	Gypsovag	3 - 28	2.5-4.5	NA
12	*Desmazeria rigida* (L.) Tutin	*Poaceae*	Graminoid	Gypsovag	< 40	1.7-2 x 0.5-0.6	1.80
13	*Diplotaxis ilorcitana* (Sennen) Aedo, Mart.-Laborde & Muñoz Garm.	*Brassicaceae*	Forb	Gypsovag	10-60	0.8-1 x 0.4-0.6	0.05
14	*Erodium cicutarium* (L.) L'Hér.	*Geraniaceae*	Forb	Gypsovag	< 50	4.5-5.5	NA
15	*Eruca vesicaria* (L.) Cav.	*Brassicaceae*	Forb	Gypsovag	20-100	1-1.4 x 0.8-1.1	NA
16	*Filago pyramidata* L.	*Asteraceae*	Forb	Gypsovag	< 44	0.5-0.8 x 0.15-0.3	6.64
17	*Galium verrucosum* Huds.	*Rubiaceae*	Forb	Gypsovag	< 50	3-4.5	0.05
18	*Hedypnois cretica* (L.) Dum. Cours.	*Asteraceae*	Forb	Gypsovag	5-40	5-8	NA
19	*Helianthemum salicifolium* (L.) Mill.	*Cistaceae*	Forb	Gypsovag	(2)3-25(30)	(0.6)0.8-1(1.2)	0.05
20	*Hippocrepis ciliata* Willd.	*Fabaceae*	Forb	Gypsovag	5-25(35)	0.5-0.7 x 2.4-2.6	0.16
21	*Hordeum murinum* L.	*Poaceae*	Graminoid	Gypsovag	(8)15-30(70)	5.7-6.3 x 1.7-2	NA
22	*Linaria arvensis* (L.) Desf.	*Scrophulariaceae*	Forb	Gypsovag	1-10	1.1-1.5 x 1.1-1.5	0.94
23	*Linum strictum* L.	*Linaceae*	Forb	Gypsovag	7-45(55)	1.1-1.6 x 0.8-0.9	0.51
24	*Lithospermum arvense* L.	*Boraginaceae*	Forb	Gypsovag	< 100	1.5-2.5	NA
25	*Narduroides salzmannii* (Boiss.) Rouy	*Poaceae*	Graminoid	Gypsovag	< 40	NA	1.20
26	*Neatostema apulum* (L.) I.M.Johnst.	*Boraginaceae*	Forb	Gypsovag	< 30	1.8-2 x 1.2-1.5	0.21
27	*Polygala monspeliaca* L.	*Polygalaceae*	Forb	Gypsovag	< 37	2.5-3 x 0.75	NA

28	*Reseda stricta* Pers.	*Resedaceae*	Forb	Gypsophyte	30-70(100)	0.9-1.4	NA
29	*Scorzonera laciniata* L.	*Asteraceae*	Forb	Gypsovag	(5)15-45(70)	1.5-3 x 15-24	NA
30	*Senecio gallicus* Chaix	*Asteraceae*	Forb	Gypsovag	< 67	2-2.5	NA
31	*Trigonella monspeliaca* L.	*Fabaceae*	Forb	Gypsovag	3-40	1.2-1.7-0.6-1	0.04
32	*Trisetum loeflinngianum* (L.) C. Presl.	*Poaceae*	Graminoid	Gypsovag	NA	NA	0.95
	Perennials						
33	*Artemisia herba-alba* Asso	*Asteraceae*	Subshrub	Gypsovag	10-50	1-1.2 x 0.5-0.6	NA
34	*Asphodelus fistulosus* L.	*Liliaceae*	Forb	Gypsovag	70	4-5.5	NA
35	*Astragalus alopecuroides* L.	*Fabaceae*	Forb	Gypsovag	30-80	NA	NA
36	*Astragalus incanus* L.	*Fabaceae*	Forb	Gypsovag	NA	2-5	NA
37	*Brachypodium retusum* (Pers.) P. Beauv.	*Poaceae*	Graminoid	Gypsovag	(12)40-60(140)	0.2	0.02
38	*Carlina corymbosa* L.	*Asteraceae*	Forb	Gypsovag	10-60	2.5-5	0.02
39	*Dipcadi serotiunum* (L.) Medik.	*Liliaceae*	Forb	Gypsovag	<40	5 x 2	NA
40	*Echinops ritro* L.	*Asteraceae*	Forb	Gypsovag	(7)22-88	6-8 x 2-2.5	NA
41	*Ephedra fragilis* Desf.	*Ephedraceae*	Shrub	Gypsovag	< 3 (4)	NA	0.34
42	*Eryngium campestre* L.	*Umbeliferae*	Subshrub	Gypsovag	(15)20-60	2.5 x 2	NA
43	*Genista scorpius* (L.) DC.	*Fabaceae*	Shrub	Gypsovag	30-200	2.1-3.2 x 2-3	NA
44	*Gypsophila struthium* Loefl. subsp. *hispanica* (Willk.) G.López	*Caryophyllaceae*	Shrub	Gypsophyte	(15)25-75(80)	0.5	0.02
45	*Hedysarum boveanum* Bunge ex Basiner	*Fabaceae*	Subshrub	Gypsovag	< 50	2.3-3	0.12
46	*Helianthemum squamatum* (L.) Pers.	*Cistaceae*	Subshrub	Gypsophyte	10-40	1.3	7.63
47	*Helianthemum syriacum* (Jacq.) Dum. Cours.	*Cistaceae*	Subshrub	Gypsovag	(2)5-50(85)	1.5	2.00
48	*Helianthemum violaceum* (Cav.) Pers.	*Cistaceae*	Subshrub	Gypsovag	(6)10-35(40)	(1.2)1.5(2)	0.18
49	*Helichrysum stoechas* (L.) Moench	*Asteraceae*	Subshrub	Gypsovag	< 70	0.4-0.5 x 0.2-0.3	2.60
50	*Herniaria fruticosa* L.	*Caryophyllaceae*	Subshrub	Gypsophyte	< 30	1 x 0.6	1.59
51	*Koeleria vallesiana* (Honck.) Gaudin	*Poaceae*	Graminoid	Gypsovag	10-40	0.4	2.00
52	*Launaea lanifera* Pau	*Asteraceae*	Subshrub	Gypsovag	< 50	0.5	0.30
53	*Linum suffruticosum* L.	*Linaceae*	Shrub	Gypsovag	< 180	2-3.4-1.1-1.7	0.23
54	*Lygeum spartum* L	*Poaceae*	Graminoid	Gypsovag	NA	10-15 x 5	0.11
55	*Moricandia arvensis* (L.) DC.	*Cruciferae*	Subshrub	Gypsovag	< 65	1.2 x 0.8	NA
56	*Ononis tridentata* L.	*Fabaceae*	Shrub	Gypsophyte	< 150	1.8-2.5(3)	0.02
57	*Plantago albicans* L.	*Plantaginaceae*	Subshrub	Gypsovag	(4)6-28(70)	2-3.5 x 1-1.5	26.38
58	*Polygala rupestris* Pourr.	*Polygalaceae*	Subshrub	Gypsovag	< 20	3-4 x 1.2-1.5	0.42
59	*Salsola vermiculata* L.	*Chenopodiaceae*	Shrub	Gypsovag	< 100	2	NA
60	*Sedum sediforme* (Jacq.) Pau	*Crassulaceae*	Subshrub	Gypsovag	< 60	0.25	0.12

61	*Sideritis hirsuta* L.	*Labiatae*	Subshrub	Gypsovag	10-69	2.3-2.7 x 1.6-2	0.12
62	*Sonchus tenerrimus* L.	*Asteraceae*	Forb	Gypsovag	NA	2.8-3.2 x 0.6-0.9	NA
63	*Stipa sp.**	*Poaceae*	Graminoid	Gypsovag	50-60	4 x 1.5	3.55
64	*Teucrium capitatum* L.	*Labiatae*	Subshrub	Gypsovag	(10)20-35(45)	1.4-2 x 0.8-1	0.18
65	*Thymus sp.**	*Labiatae*	Subshrub	Gypsovag	10-40	0.5-0.8	0.97

**Stipa sp*. can be either *Stipa lagascae* Roem. & Schult. or *Stipa parviflora* Desf. and *Thymus sp.* can be either *Thymus vulgaris* L. or *Thymus zygis* L. (grouped because the identification at the seedling stage was challenging). Growth habits classification taken from USDA-NRCS (https://plants.usda.gov/). Plant height and seed size were obtained mainly from "Flora Ibérica" (http://www.anthos.es/), "Herbario de Jaca" (http://floragon.ipe.csic.es/), and "Flora Vascular" (https://www.floravascular.com/), but in some cases, when there were not available data, seed size was estimated using graph paper (n=10). Total density of plants found in above-ground vegetation surveys (May 2014), recorded under the canopy of 25 random individuals of the same target species in the study area (see Foronda et al. 2019 for more details in the methodology). NA=Not Available (found in the study site but not recorded in vegetation surveys).

Appendix 2. Target species and soil seed bank survey

Table S.2 Relative abundance (%) of shrubs and subshrubs recorded in the study site.

Species	**Family**	**Growth habit**	**Gypsophily**	**Plant height (cm)**	**Architecture**	**Relative Abundance**
Artemisia herba-alba	*Asteraceae*	Subshrub	Gypsovag	10-50	Crawling-branched	0.53
Ephedra fragilis	*Ephedraceae*	Shrub	Gypsovag	< 3 (4)	Erect	NA
Eryngium campestre	*Umbeliferae*	Subshrub	Gypsovag	(15)20-60	Erect	0.04
Genista scorpius	*Fabaceae*	Shrub	Gypsovag	30-200	Erect	NA
Gypsophila struthium subsp. *hispanica* *	*Caryophyllaceae*	Shrub	Gypsophyte	(15)25-75(80)	Crawling-branched	3.39
Hedysarum boveanum	*Fabaceae*	Subshrub	Gypsovag	< 50	Erect	0.09
Helianthemum squamatum *	*Cistaceae*	Subshrub	Gypsophyte	10-40	Crawling-branched	31.45
Helianthemum syriacum	*Cistaceae*	Subshrub	Gypsovag	(2)5-50(85)	Erect	NA
Helianthemum violaceum	*Cistaceae*	Subshrub	Gypsovag	(6)10-35(40)	Erect	2.23
Helichrysum stoechas	*Asteraceae*	Subshrub	Gypsovag	< 70	Erect	6.28
Herniaria fruticosa	*Caryophyllaceae*	Subshrub	Gypsophyte	< 30	Crawling-branched	12.87
Launaea lanifera	*Asteraceae*	Subshrub	Gypsovag	< 50	Crawling-branched	0.04
Linum suffruticosum	*Linaceae*	Shrub	Gypsovag	< 180	Erect	0.13
Moricandia arvensis	*Cruciferae*	Subshrub	Gypsovag	< 65	Crawling-branched	NA
*Ononis tridentata**	*Fabaceae*	Shrub	Gypsophyte	< 150	Erect	0.80
Plantago albicans	*Plantaginaceae*	Subshrub	Gypsovag	(4)6-28(70)	Erect	25.84
Polygala rupestris	*Polygalaceae*	Subshrub	Gypsovag	< 20	Erect	NA
Salsola vermiculata	*Chenopodiaceae*	Shrub	Gypsovag	< 100	Crawling-branched	0.40
Sedum sediforme	*Crassulaceae*	Subshrub	Gypsovag	< 60	Erect	0.18
Sideritis hirsuta	*Labiatae*	Subshrub	Gypsovag	10-69	Erect	1.16
Teucrium capitatum	*Labiatae*	Subshrub	Gypsovag	(10)20-35(45)	Erect	0.53
Thymus vulgaris *	*Labiatae*	Subshrub	Gypsovag	10-40	Erect	9.09
Thymus zygis	*Labiatae*	Subshrub	Gypsovag	10-30	Erect	4.94

* indicate the selected target species. Relative abundance (%) per species was recorded in six paralleled 250-m transects arranged in the study site in May 2010. NA = Not Available (present in the study site but not recorded in the vegetation survey).

Table S.3 Height and canopy area of each of 25 individuals per target species randomly selected in the study site (La Lomaza de Belchite).

	G. struthium		***O. tridentata***		***H. squamatum***		***T. vulgaris***	
Individual	Height (m)	Area (m^2)	Height (m)	Area (m^2)	Height (m)	Area (m^2)	Height (m)	Area (m^2)
1	0.39	0.90	0.36	0.21	0.27	0.17	0.33	0.43
2	0.58	1.15	0.70	0.42	0.28	0.08	0.30	0.22
3	0.42	0.67	0.49	0.37	0.20	0.11	0.35	0.06
4	0.52	0.64	0.66	0.52	0.17	0.05	0.29	0.15
5	0.58	0.47	0.60	0.41	0.20	0.06	0.33	0.15
6	0.32	0.68	0.51	0.66	0.14	0.10	0.17	0.08
7	0.37	0.77	0.54	0.24	0.10	0.06	0.25	0.10
8	0.60	0.77	0.43	0.23	0.23	0.15	0.40	0.28
9	0.35	0.41	0.58	0.42	0.18	0.05	0.16	0.09
10	0.60	0.64	0.47	0.32	0.29	0.05	0.24	0.14
11	0.57	1.12	0.55	0.41	0.20	0.11	0.24	0.04
12	0.34	0.62	0.38	0.57	0.29	0.14	0.18	0.06
13	0.48	0.32	0.62	0.29	0.20	0.23	0.32	0.16
14	0.49	0.53	0.32	0.26	0.25	0.12	0.23	0.19
15	0.72	1.80	0.58	0.35	0.15	0.12	0.19	0.09
16	0.57	0.65	0.53	0.44	0.16	0.12	0.31	0.13
17	0.46	0.49	0.37	0.32	0.22	0.12	0.17	0.11
18	0.28	0.62	0.45	0.19	0.26	0.13	0.17	0.10
19	0.35	0.69	0.42	0.18	0.24	0.11	0.16	0.07
20	0.41	0.69	0.50	0.18	0.24	0.08	0.22	0.08
21	0.34	0.51	0.51	0.45	0.12	0.06	0.27	0.02
22	0.25	0.56	0.53	0.52	0.13	0.04	0.22	0.06
23	0.67	1.68	0.70	0.29	0.21	0.11	0.22	0.10
24	0.47	0.69	0.62	0.64	0.18	0.06	0.30	0.07
25	0.67	0.79	0.85	1.14	0.24	0.14	0.23	0.07
Average ± SE	0.47 ± 0.03	0.75 ± 0.07	0.53 ± 0.02	0.40 ± 0.04	0.21 ± 0.01	0.10 ± 0.01	0.25 ± 0.01	0.12 ± 0.02

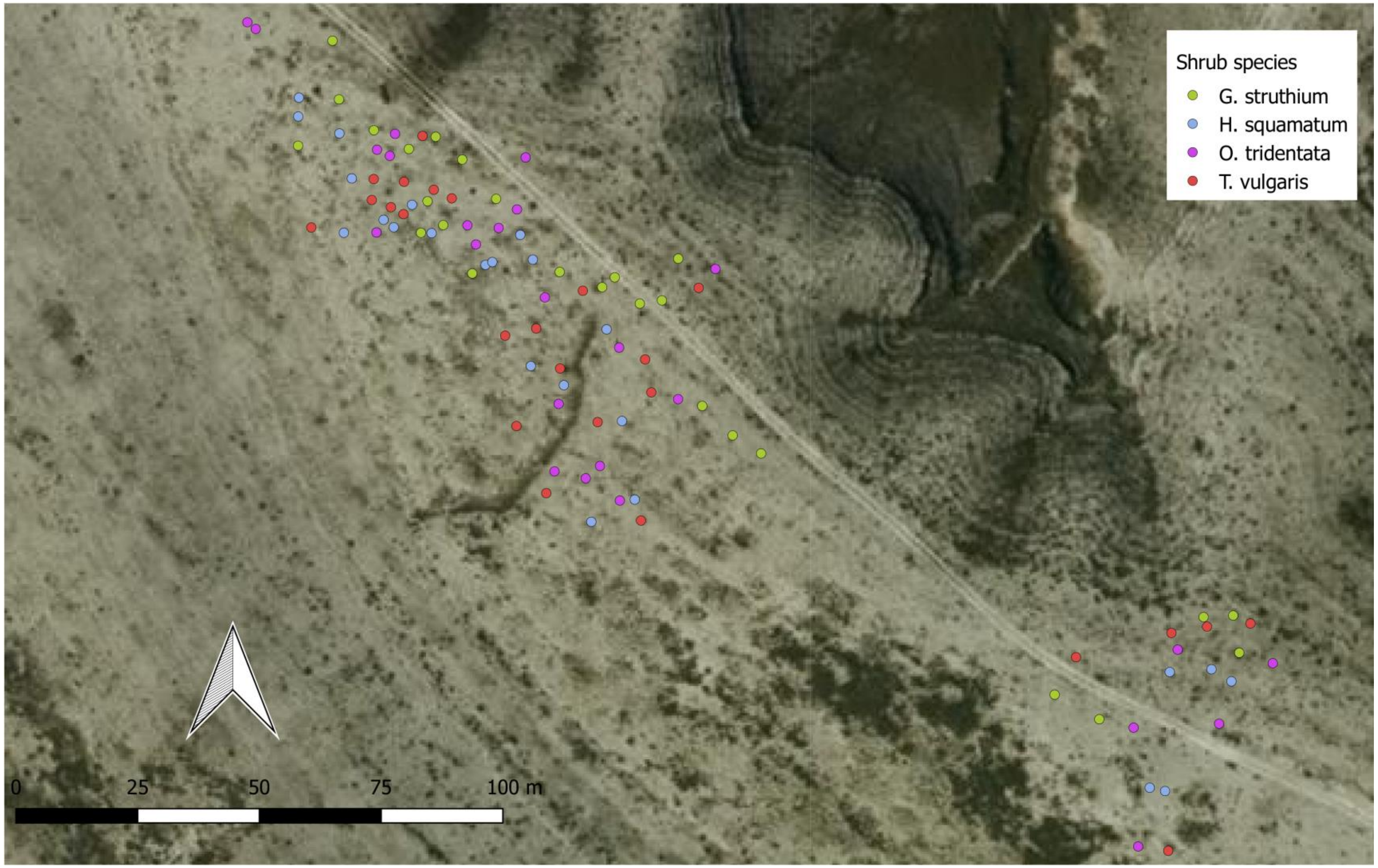

Fig. S1 Spatial distribution of the 25 individuals per target species sampled in the study site (La Lomaza de Belchite).

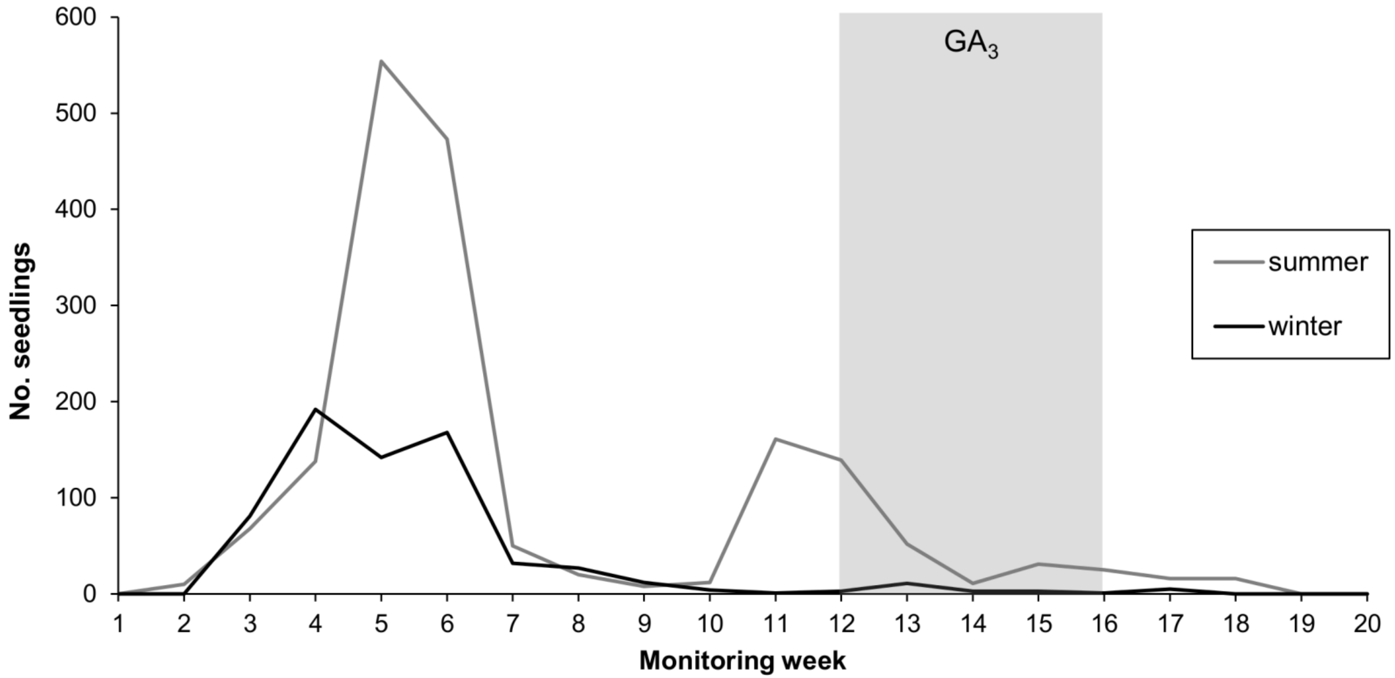

Fig. S.2 Total number of new seedlings (germinated seeds) recorded per monitoring week in winter and summer samples separately. Grey shading represents the period in which trays were irrigated with a gibberellic acid solution (GA_3).

Appendix 3. Perennials in the persistent soil seed bank

Table S.4 Results of GLMs to test the effect of the microsite, the target species and the plant height, and the interaction among variables on soil seed bank richness and abundance of perennials emerged in the persistent soil seed bank.

Dependent variables	Explanatory variables	DF	Deviance	p-value
Richness	Microsite	2	116.974	**<0.001**
	Target species	3	6.668	0.083
	Plant height	1	0.751	0.386
	Microsite : Target species	6	3.342	0.765
	Microsite : Plant height	2	0.261	0.878
	Target species : Plant height	3	7.935	**<0.05**
	Microsite : Target species : Plant height	6	5.120	0.529
Abundance	Microsite	2	559.41	**<0.001**
	Target species	3	64.95	**<0.001**
	Plant height	1	9.67	**<0.01**
	Microsite : Target species	6	59.25	**<0.001**
	Microsite : Plant height	2	20.00	**<0.001**
	Target species : Plant height	3	28.02	**<0.001**
	Microsite : Target species : Plant height	6	23.68	**<0.001**

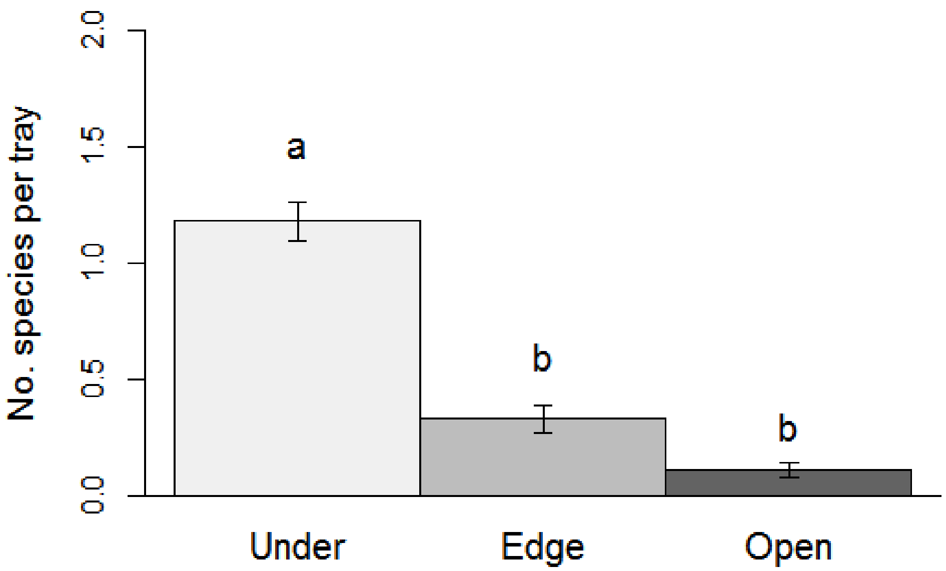

Fig. S.3 Mean richness of perennials per tray at each microsite (under shrub canopy, at the edge of the shrub and in open areas) in the persistent seed bank; Different letters indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite were found in GLMs with Poisson error distribution ($p \leq 0.05$).

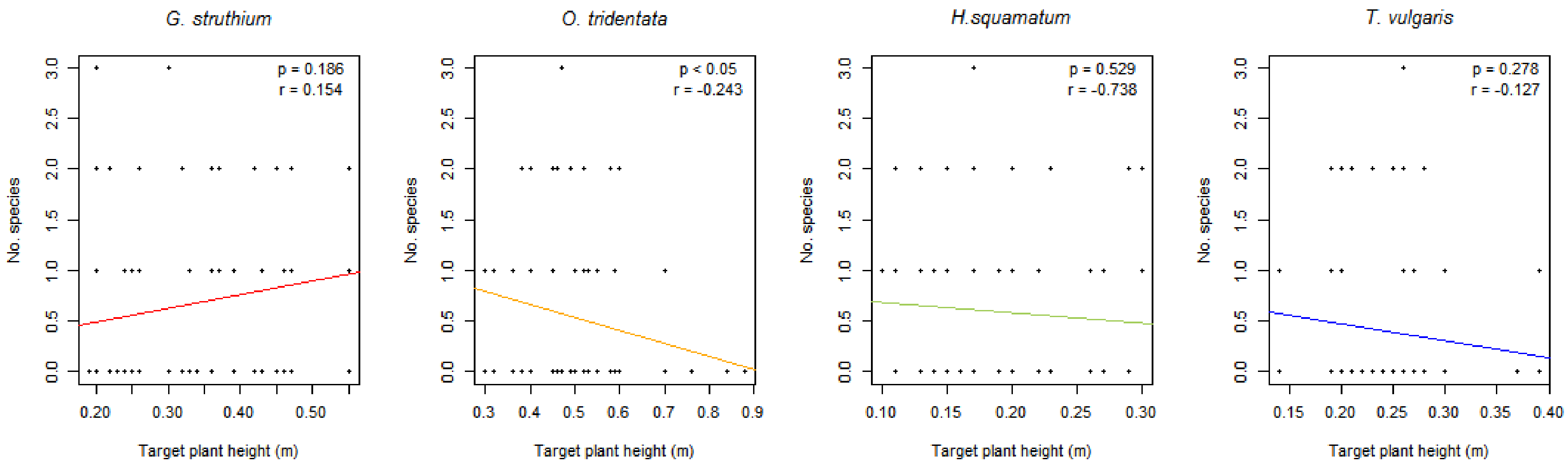

Fig. S.4 Correlations between richness of perennials and the plant height (m) per target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) in the persistent seed bank. p≤0.05 indicates significant effects of the plant height (r = Pearson's correlations).

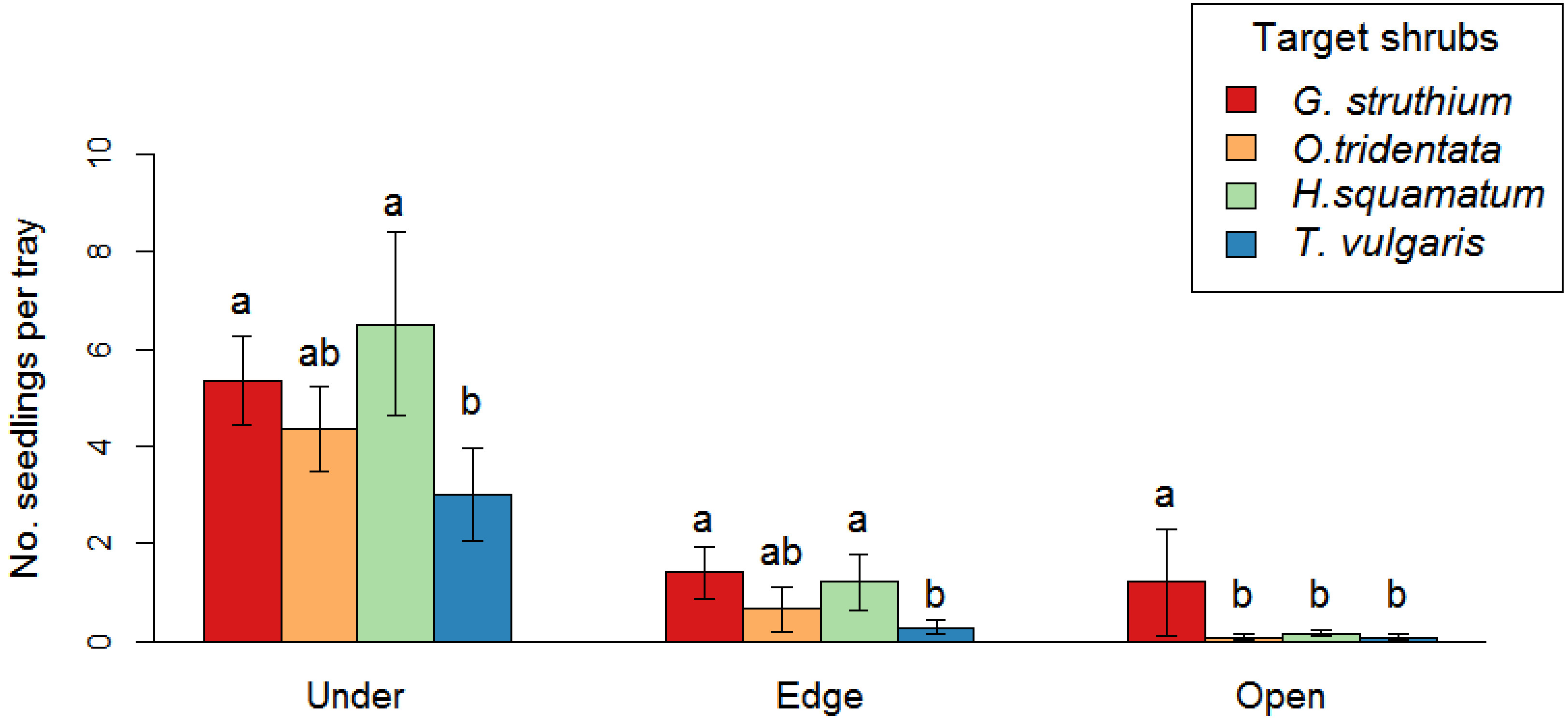

Fig. S.5 Mean abundance of perennials per tray in each target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) per microsite (under shrub canopy, at the edge of the shrub and in open areas) in the persistent seed bank; Different letters indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite were found in GLMs with Poisson error distribution ($p \leq 0.05$).

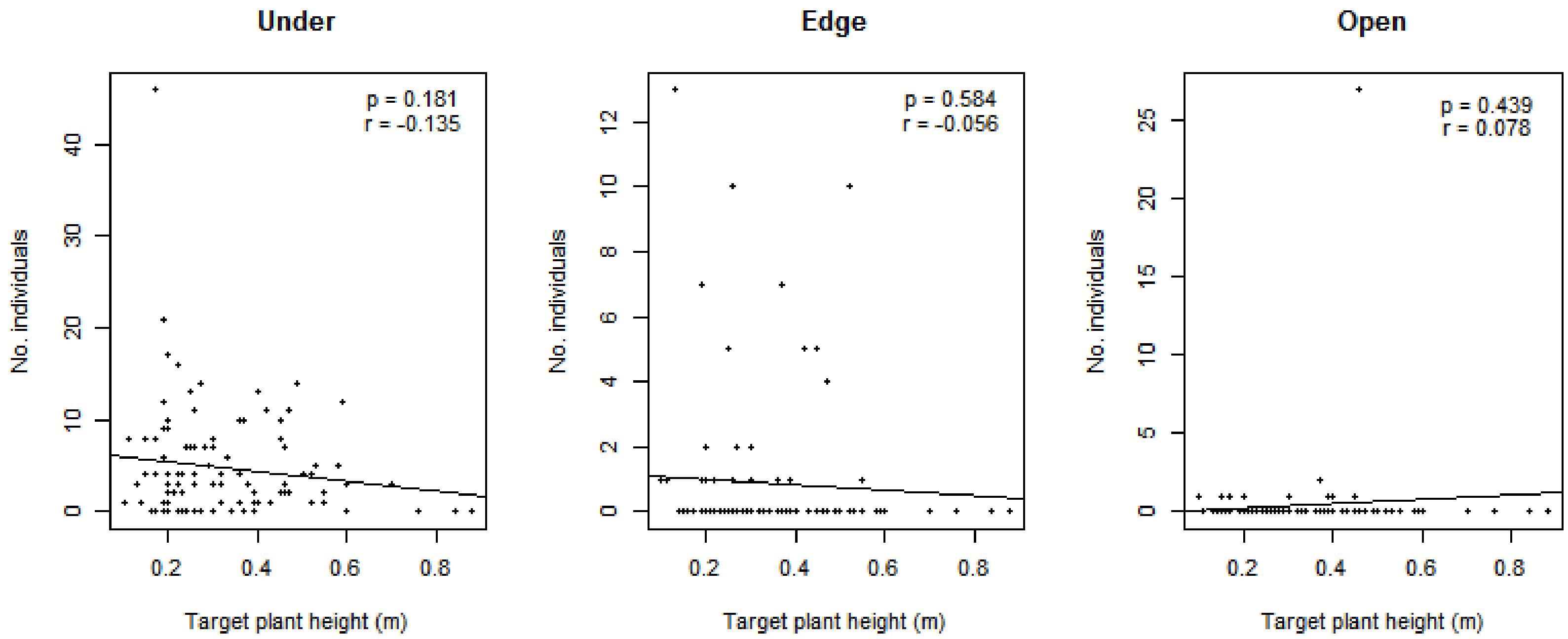

Fig. S.6 Correlations between abundance of perennials and the plant height (m) per microsite (under the shrub canopy, at the edge of the shrub and in open areas) in the persistent seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

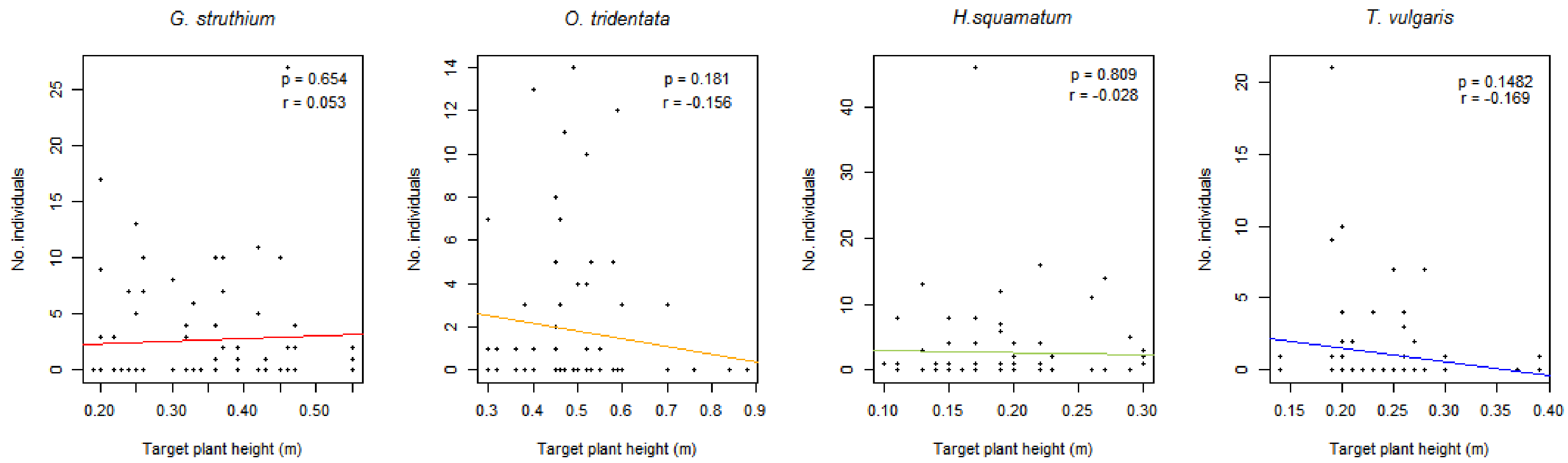

Fig. S.7 Correlations between abundance of perennials and the plant height (m) per target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) in the persistent seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

<u>Appendix 4.</u> Annuals in the complete soil seed bank

Table S.5 Results of GLMs to test the effect of the microsite, the target species and the plant height, and the interaction among variables on soil seed bank richness and abundance for annuals emerged in the complete soil seed bank.

Dependent variables	Explanatory variables	DF	Deviance	p-value
Richness				
	Microsite	2	54.89	**<0.001**
	Target species	3	9.14	**<0.05**
	Plant height	1	5.60	**<0.05**
	Microsite : Target species	6	2.62	0.854
	Microsite : Plant height	2	0.65	0.722
	Target species : Plant height	3	7.09	0.069
	Microsite : Target species : Plant height	6	1.67	0.948
Abundance				
	Microsite	2	113.06	**<0.001**
	Target species	3	40.01	**<0.001**
	Plant height	1	14.11	**<0.001**
	Microsite : Target species	6	25.94	**<0.001**
	Microsite : Plant height	2	4.993	0.082
	Target species : Plant height	3	42.74	**<0.001**
	Microsite : Target species : Plant height	6	8.62	0.196

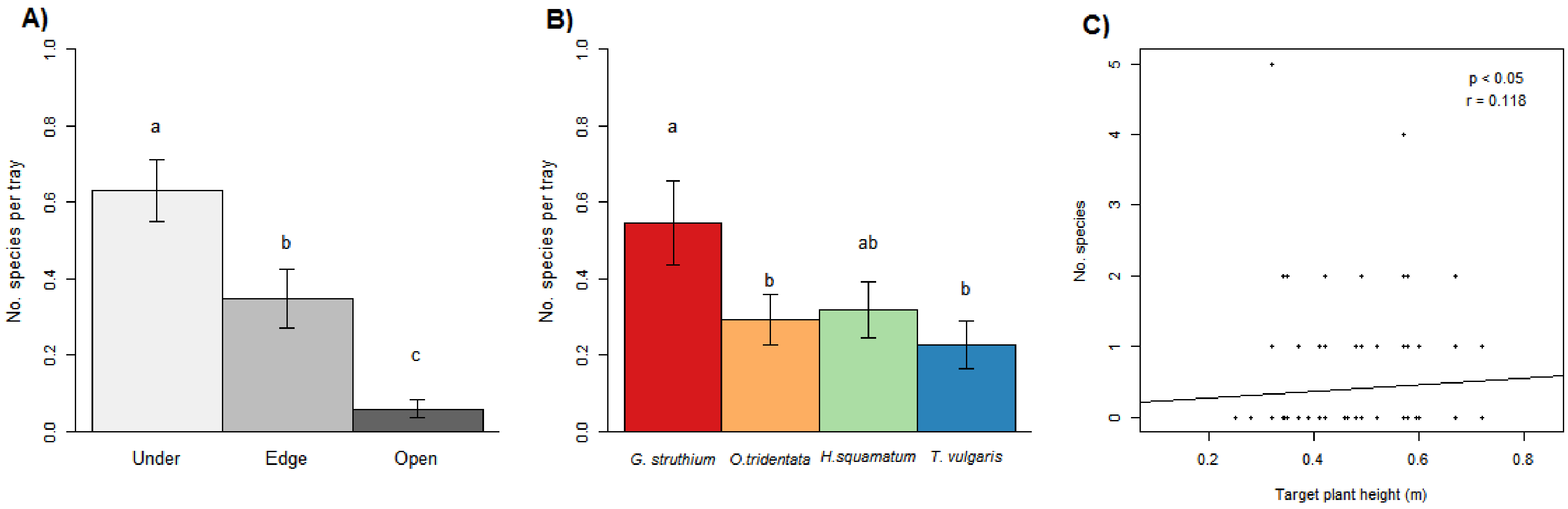

Fig. S.8 A) Mean richness of annuals per tray at each microsite (under shrub canopy, at the edge of the shrub and in open areas) in the complete seed bank; **B)** Mean richness of annuals per tray associated with each target species (*G. struthium*, *O. tridentata*, *H. squamatum and T. vulgaris*) in the complete seed bank; **C)** Correlations between richness of annuals and the plant height (m) in the complete seed bank. Different letters in A and B indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite or the target species were found in GLMs with Poisson error distribution ($p \leq 0.05$). In C, $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

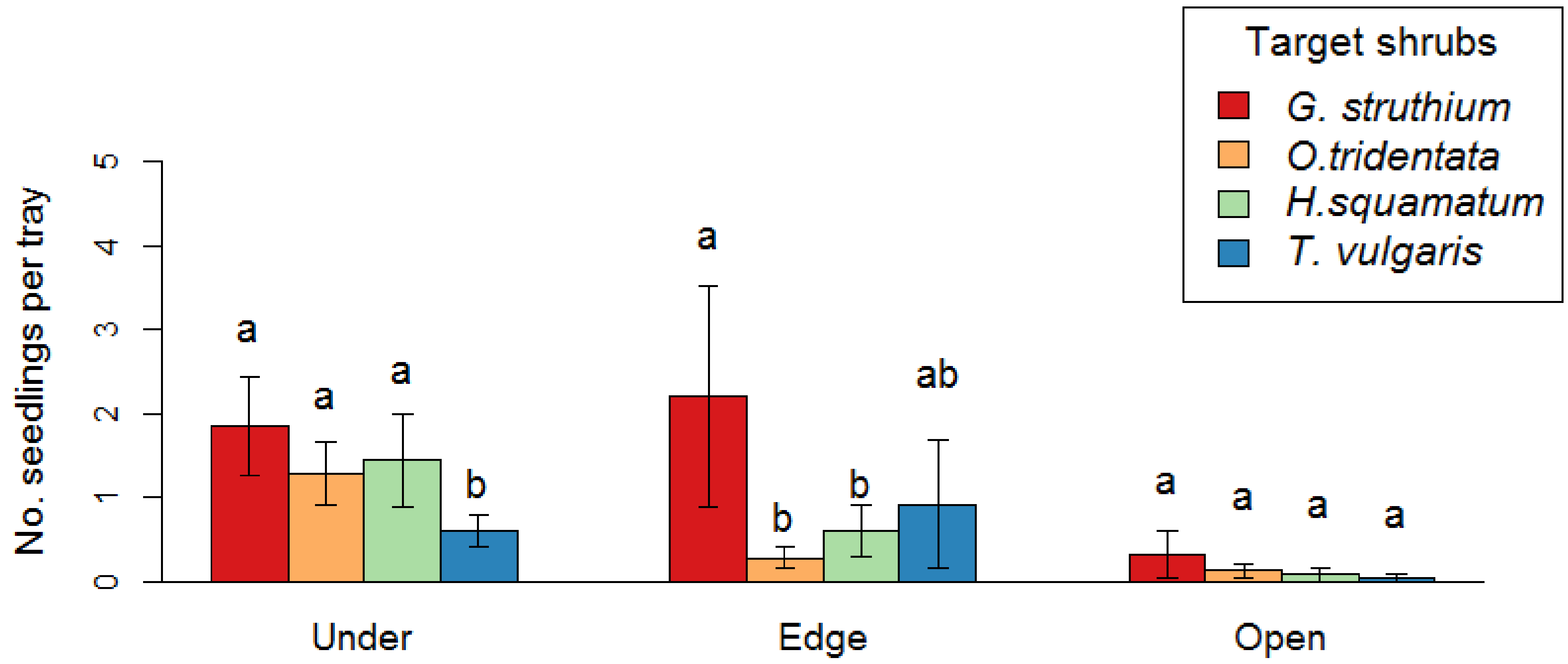

Fig. S.9 Mean abundance of annuals per tray in each target species (*G. struthium, O. tridentata, H. squamatum* and *T. vulgaris*) per microsite (under shrub canopy, at the edge of the shrub and in open areas) in the complete seed bank; Different letters indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite were found in GLMs with Poisson error distribution ($p \leq 0.05$).

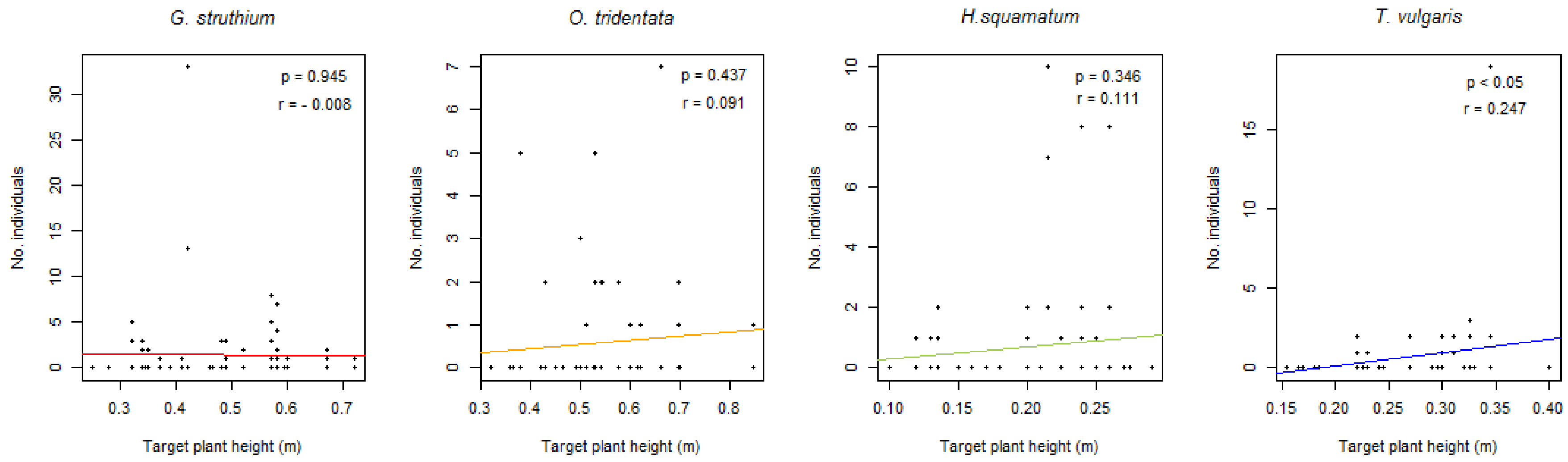

Fig. S.10 Correlations between abundance of annuals and the plant height (m) per target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) in the complete seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

<u>Appendix 5.</u> Annuals in the persistent soil seed bank

Table S.6 Results of GLMs to test the effect of the microsite, the target species and the plant height, and the interaction among variables on soil seed bank richness and abundance for annuals emerged in both the persistent soil seed bank.

Dependent variables	Explanatory variables	DF	Deviance	p-value
Richness				
	Microsite	2	9.868	**<0.01**
	Target species	3	3.229	0.357
	Plant height	1	6.551	**<0.05**
	Microsite : Target species	6	9.105	0.168
	Microsite : Plant height	2	0.594	0.743
	Target species : Plant height	3	1.968	0.579
	Microsite : Target species : Plant height	6	0.579	0.997
Abundance				
	Microsite	2	12.084	**<0.01**
	Target species	3	9.633	**<0.05**
	Plant height	1	8.787	**<0.01**
	Microsite : Target species	6	11.704	0.069
	Microsite : Plant height	2	6.726	**<0.05**
	Target species : Plant height	3	3.431	0.330
	Microsite : Target species : Plant height	6	0.697	0.995

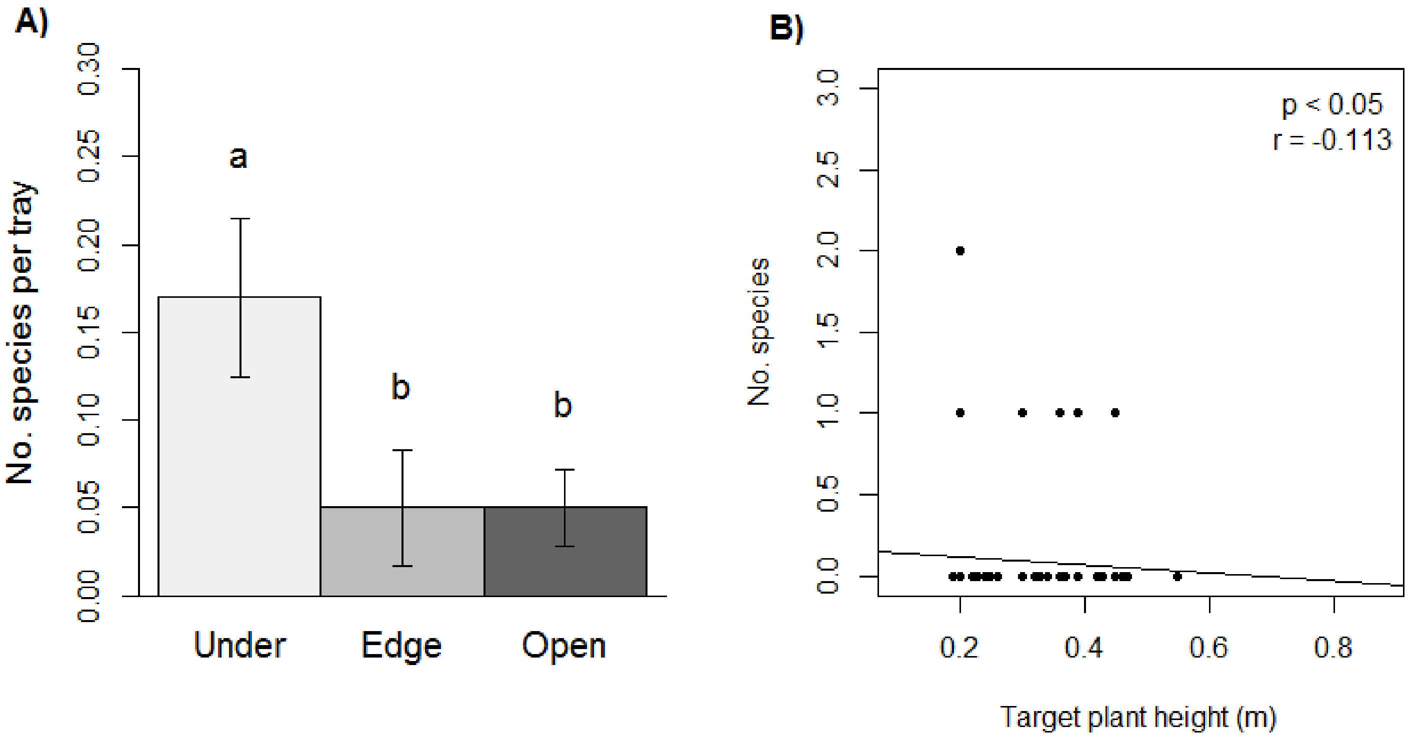

Fig. S.11 A) Mean richness of annuals per tray at each microsite (under shrub canopy, at the edge of the shrub and in open areas) in the persistent seed bank. Different letters indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite were found in GLMs with Poisson error distribution ($p \leq 0.05$); **B)** Correlations between abundance of annuals and the plant height (m) in the persistent seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

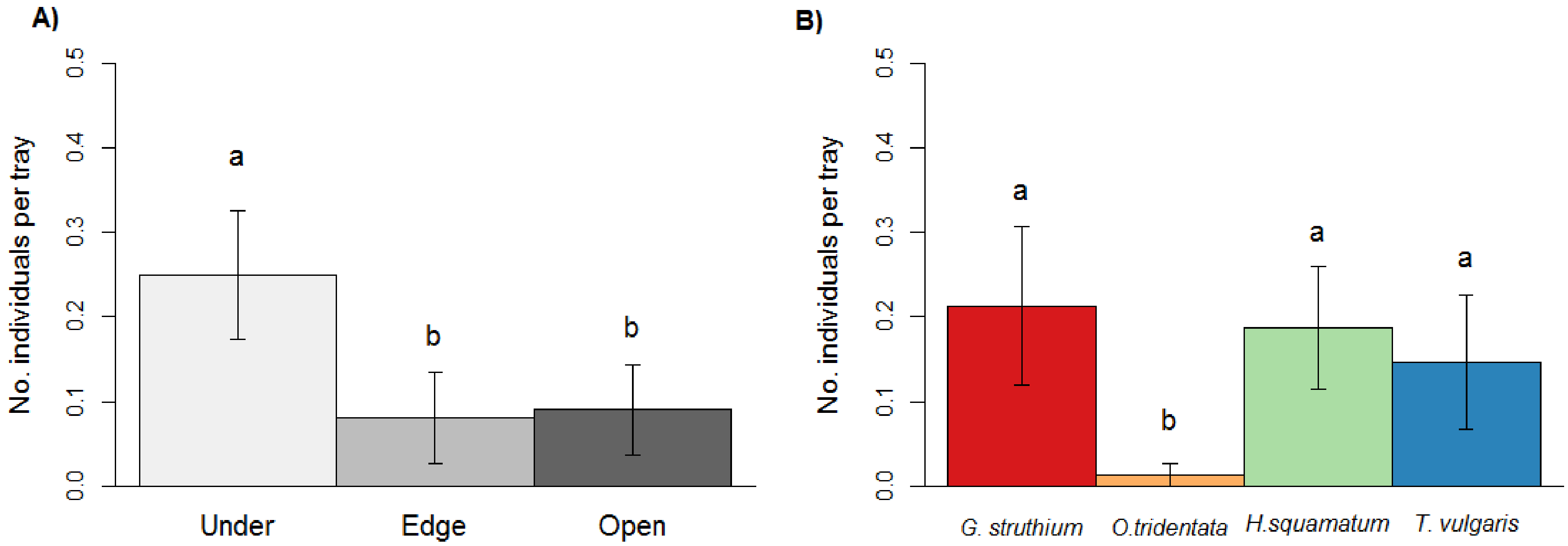

Fig. S.12 A) Mean abundance of annuals per tray at each microsite (under shrub canopy, at the edge of the shrub and in open areas) in the persistent seed bank; **B)** Mean abundance of annuals per tray associated with each target species (*G. struthium, O. tridentata, H. squamatum and T. vulgaris*) in the persistent seed bank. Different letters indicate significant differences after Tukey's multiple comparisons when significant effects of the microsite or the target species were found in GLMs with Poisson error distribution ($p \leq 0.05$).

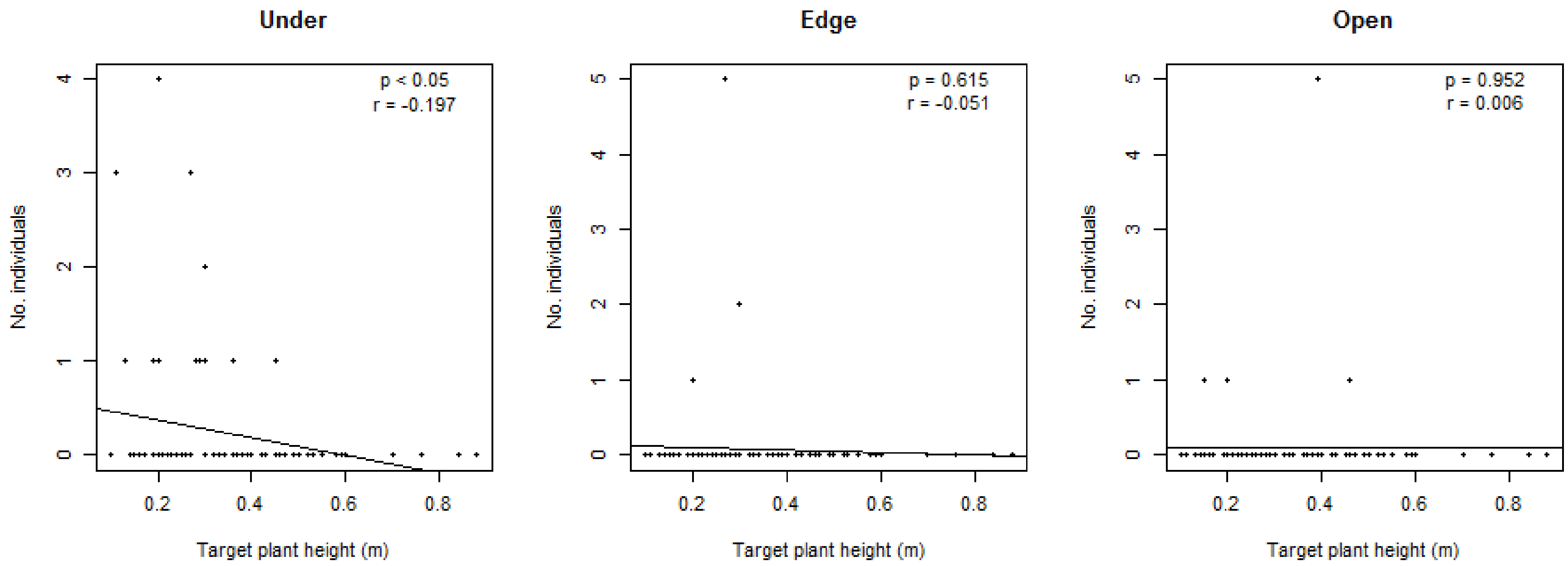

Fig. S.13 Correlations between abundance of annuals and the plant height (m) per target species (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) in the persistent seed bank. $p \leq 0.05$ indicates significant effects of the plant height (r = Pearson's correlations).

<u>Appendix 6.</u> Species composition in the soil seed bank *vs*. species composition in above-ground vegetation

Table S7. Density (individuals/m^2) of seeds and emerged individuals per species recorded in the complete soil seed bank and vegetation surveys at each microsite (open areas and canopy = edge + under) per target shrub.

Target shrub	***G. struthium***				***H. squamatum***				***O. tridentata***				***T. vulgaris***			
Community compartment	**Seed bank**		**Aboveground**		**Seed bank**		**Aboveground**		**Seed bank**		**Aboveground**		**Seed bank**		**Aboveground**	
Microsite	**open**	**canopy**	**open**	**canopy**	**open**	**Canopy**	**open**	**canopy**	**open**	**canopy**	**open**	**canopy**	**open**	**canopy**	**open**	**canopy**
<u>Annuals</u>																
Aegilops geniculata Roth.	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alyssum alyssoides (L.) L.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anagallis arvensis L.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asterolinon linum-stellatum (L.) Duby	0.0	207.9	1.2	47.5	0.0	41.6	54.5	23.7	0.0	0.0	0.4	29.4	0.0	0.0	1.0	2.9
Brachypodium distachyon (L.) P. Beauv.	0.0	0.0	0.0	2.1	0.0	0.0	0.0	2.6	0.0	0.0	0.6	0.9	0.0	0.0	0.0	0.6
Bromus rubens L.	0.0	0.0	0.2	3.3	0.0	0.0	0.0	1.4	0.0	41.6	0.0	2.4	0.0	0.0	0.0	6.0
Bupleurum semicompositum L.	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Campanula fastigiata Dufour ex A. DC	0.0	41.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cerastium pumilum Curtis	0.0	0.0	0.8	26.1	0.0	0.0	69.7	9.7	0.0	41.6	0.6	4.1	0.0	0.0	0.0	3.6
Chaenorrhinum rubrifolium (Robill. & Castagne ex DC.) Fourr.	291.0	3326.0	0.0	0.3	83.2	1579.9	51.1	0.0	124.7	1330.4	0.0	0.0	41.6	1330.4	0.0	0.0
Clypeola jonthlaspi L.	0.0	0.0	0.0	0.0	0.0	41.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmazeria rigida (L.) Tutin	0.0	0.0	0.0	4.7	0.0	0.0	0.0	5.6	0.0	0.0	0.2	0.9	0.0	0.0	0.0	2.6
Diplotaxis ilorcitana (Sennen) Aedo, Mart.-Laborde & Muñoz Garm.	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Filago pyramidata L.	0.0	374.2	0.4	16.9	0.0	374.2	28.9	16.3	0.0	83.2	0.7	5.0	0.0	166.3	3.9	4.0
Galium verrucosum Huds.	0.0	41.6	0.0	2.3	0.0	0.0	34.0	0.0	0.0	41.6	0.0	0.0	0.0	83.2	0.0	0.0
Hippocrepis ciliata Willd.	0.0	0.0	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Linaria arvensis (L.) Desf.	0.0	0.0	0.0	2.9	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.9
Linum strictum L.	0.0	207.9	0.0	0.9	0.0	41.6	0.0	0.8	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Narduroides salzmannii (Boiss.) Rouy	0.0	0.0	0.3	5.2	0.0	0.0	17.0	0.9	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Neatostema apulum (L.) I.M.Johnst.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Reseda stricta Pers.*Reseda stricta*	41.6	0.0	0.0	0.0	0.0	41.6	0.0	1.1	0.0	41.6	0.1	0.5	0.0	0.0	0.0	1.9
Trigonella monspeliaca L.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Trisetum loeflinngianum (L.) C. Presl.	0.0	0.0	0.0	2.6	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Unknown anual	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
<u>Perennials</u>																
Brachypodium retusum (Pers.) P. Beauv.	41.6	0.0	1.2	2.4	0.0	83.2	0.0	0.0	41.6	41.6	1.1	0.2	0.0	83.2	0.0	0.0
Carduus sp.	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Ephedra fragilis Desf.	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8
Gypsophila struthium Loefl. subsp. *hispanica* (Willk.) G.López	0.0	249.5	0.0	0.0	0.0	83.2	0.0	0.0	0.0	83.2	0.0	0.1	0.0	83.2	0.0	0.0
Hedysarum boveanum Bunge ex Basiner	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Helianthemum syriacum (Jacq.) Dum. Cours	0.0	166.3	0.9	4.6	0.0	41.6	0.0	0.0	0.0	374.2	0.4	2.4	0.0	291.0	0.2	5.7
Helianthemum violaceum (Cav.) Pers.	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Helianthemum squamatum (L.) Pers.	83.2	498.9	6.0	12.6	41.6	2120.3	3.2	4.0	0.0	1081.0	5.9	7.2	41.6	789.9	0.5	4.2
Helichrysum stoechas (L.) Moench	249.5	1288.8	0.7	3.1	0.0	831.5	0.0	0.5	83.2	956.2	1.7	4.9	124.7	997.8	0.0	2.7
Herniaria fruticosa L.	623.6	10269.1	1.3	1.5	207.9	13678.2	1.4	2.7	249.5	13719.8	1.2	2.0	457.3	6818.3	0.0	8.9
Koeleria vallesiana (Honck.) Gaudin	0.0	41.6	0.9	3.3	0.0	41.6	0.0	0.0	0.0	83.2	0.9	2.1	0.0	41.6	0.8	3.3
Launaea lanifera Pau	0.0	0.0	0.0	0.8	0.0	207.9	0.0	0.0	0.0	41.6	0.2	0.2	0.0	41.6	0.0	1.1
Linum suffruticosum L.	0.0	207.9	0.0	0.1	0.0	41.6	0.0	0.0	0.0	41.6	0.1	0.9	0.0	41.6	0.0	0.0
Lygeum spartum L	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Moricandia arvensis (L.) DC.	0.0	41.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ononis tridentata L.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plantago albicans L.	0.0	207.9	16.2	47.9	0.0	457.3	29.3	50.9	0.0	83.2	15.7	26.0	0.0	83.2	19.6	13.2
Polygala rupestris Pourr.	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	6.5	0.0
Sedum sediforme (Jacq.) Pau	83.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	41.6	0.0	0.1	0.0	0.0	0.0	0.0
Sideritis hirsuta L.	0.0	41.6	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	41.6	0.0	0.5
Sonchus tenerrimus L.	0.0	41.6	0.0	0.0	0.0	166.3	0.0	0.0	0.0	124.7	0.0	0.0	0.0	83.2	0.0	0.0
Stipa sp.	0.0	415.8	5.1	34.5	0.0	83.2	0.0	0.8	0.0	41.6	3.3	15.4	0.0	415.8	0.0	0.0
Teucrium capitatum L.	0.0	83.2	0.0	0.3	0.0	0.0	0.0	0.0	0.0	124.7	0.0	0.4	0.0	0.0	0.0	0.9
Thymus sp.	41.6	249.5	4.5	20.0	0.0	374.2	0.0	0.0	0.0	1330.4	0.0	5.4	41.6	1663.0	0.0	0.0

Density of plants found in a vegetation survey performed in spring 2014 in the same study site (the same location of an area smaller than 0.5 km^2). We recorded annuals and perennials occurring under the canopy of 25 random individuals per target species (‘canopy’ microsite = ‘under’ + ‘edge’ microsites). Sampled areas were circular plots defined by plastic rings of variable size matching the canopy area of each sampled individual. We also surveyed the vegetation in the surrounding open areas (‘open’ microsite) in paired circular plots of the same size than the sampled individual, and placed randomly in the north direction 50 cm away from each sampled individual. The total number of rings was 200 (4 target species x 25 individuals x 2 microsites). See Foronda et al. 2019 for more details.

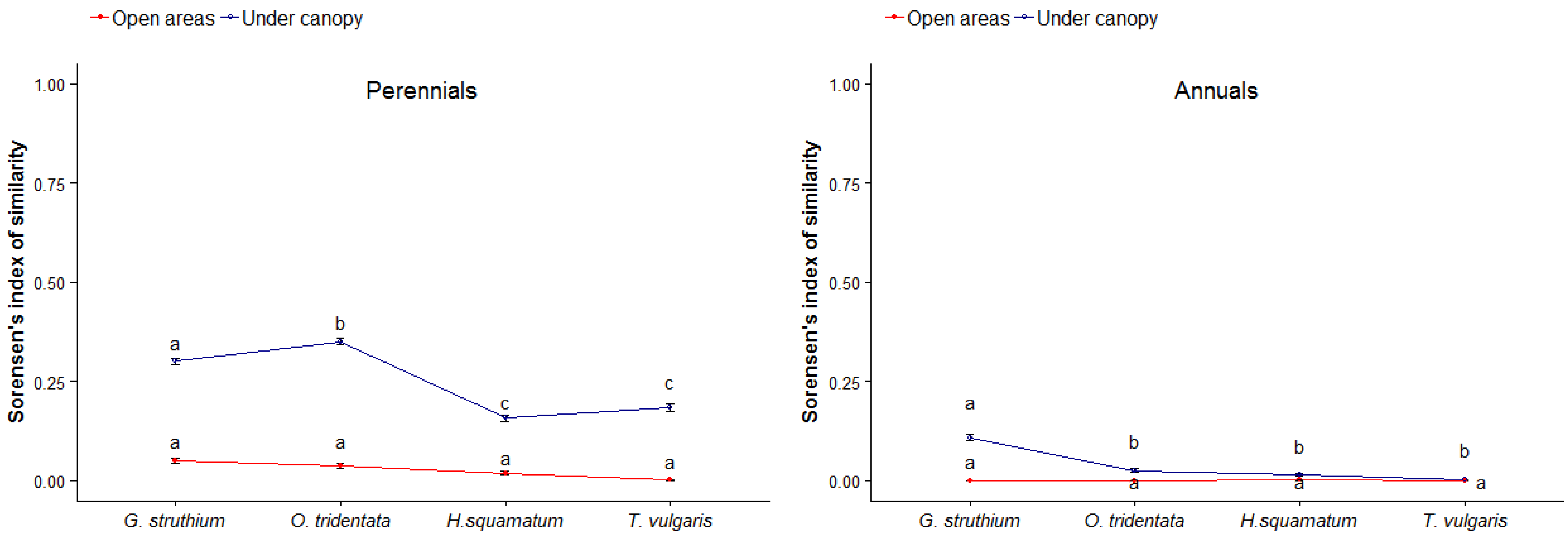

Fig. S.14 Mean Sorensen's index of similarity (SSI) in species composition between the complete soil seed bank (perennials and annuals separately) and the aboveground vegetation recorded under target species canopies (*G. struthium*, *O. tridentata*, *H. squamatum* and *T. vulgaris*) and in the paired open areas. Different letters indicate significant differences among target species after Kruskal-Wallis multiple comparisons ($p<0.05$).