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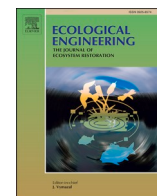
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Trifolium subterraneum as a potential nurse plant for restoring soil and Mediterranean grasslands after quarry exploitation in Lebanon

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ABSTRACT

Destruction of Mediterranean herbaceous communities resulting from quarry exploitation exacerbates the need for their ecological restoration. By facilitating the growth and development of other plant species, nurse plants can be used to speed up regeneration processes. Nevertheless, differences in soil properties and co-existing species may change plant interactions from facilitation to competition. This study evaluated interactions of a potential nurse species, *Trifolium subterraneum* L., in a 2-years ex situ mesocosm experiment. During the first year, soils collected from a former quarry and a nearby dry-grassland were planted in pots with *T. subterraneum* alone or with four individuals of four target species (*Aegilops triuncialis* L., *Echinops viscosus* L., *Eryngium creticum* Lam., *Hyoscyamus aureus* L.) characteristics of Mediterranean grasslands. In the second year, the same experiment was repeated following the incorporation of dried *T. subterraneum* biomass into the soil. Soil analyses were done before initiating the experiment from both reference and degraded soil, after the first and the second growing season. Index of Relative Interaction Intensity (RII) was calculated for several plant traits enabling the measuring of the plants' competitive ability. Our results show that, before starting the experiment, soils collected from both the reference and degraded sites were significantly different (e.g. CEC, pH, P₂O₅, MgO, N, C, Clay). These differences were still notable throughout the first growing season. Nevertheless, after the second growing season and when dried *T. subterraneum* biomass was incorporated into the soil, a significant increase in soil fertility (e.g. N, C, C:N, P₂O₅) was measured. For plants, during the first growing season, RII figures amidst competition dominating interactions. Facilitation was apparent only between the biomass of *T. subterraneum* pure seed mix in both degraded and reference soil. During the second growing season, *T. subterraneum* also performed better alone, especially on degraded soils. Nevertheless, because of its facilitative effects on biomass and surface cover when cultivated as a pure stand, *T. subterraneum* can be recommended as a nurse species for re-establishing soil fertility of degraded quarries as a first step of ecological restoration.

1. Introduction

Although the Mediterranean ecosystems represent less than 5 % of world terrestrial ecosystems, they exhibit high local biodiversity (Vilà and Sardans, 1999). Due to its location, topography, and altitude, Lebanon's highly diverse ecosystem is considered a biodiversity hotspot in the Mediterranean Basin (Myers et al., 2000). Relative to its size, Lebanon has one of the highest densities of floral diversity in the Mediterranean basin (Médail and Quézel, 1997). This study is particularly concerned with the Mediterranean dry grasslands of Lebanon, which are part of about 4.5 million s.q.m. of lands in the Near East region classified

as permanent pastures, and are within the Pre-Steppic Mediterranean Ensemble (MoA, 1996). Most of these grasslands are distributed on poor soils in the semi-arid and arid areas with non-uniformity in both rainfall distribution and amount, along with centuries of grazing practices (Buisson et al., 2020; Mahy et al., 2024). Such factors would render the ecosystem of low resilience when faced with exogenous perturbations such as quarry exploitation (Chenot et al., 2017; Shaiban et al., 2021).

Quarry exploitation has grown exponentially in Lebanon due to years of unregulated chaotic mining activity. Although the number of quarries on the Lebanese territory is variable and depends on the source, there are approximately 1300 quarries dispersed all over Lebanon and almost

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75 % of these quarries are present in sparse grasslands and bare rocky lands, significantly affecting their sustainable management (Darwish et al., 2011). Those are causing damage to existing arable lands, accelerating erosion processes, modifying ecosystems, destroying natural habitat, interrupting natural successions and changing landscape patterns (Khater et al., 2003).

Interactions between plant species ranging from competition to neutral-uninvolved interactions to facilitation are significant driving forces in plant community restoration (Brooker et al., 2008). In this context, some plant species have been qualified as “nurse plants” and defined as plants that can facilitate the growth and development of other plants through positive interaction (Padilla and Pugnaire, 2006; Saby et al., 2024). Such plants can play a crucial role in recovering structures and functions of some ecosystems since they are a driving force in the succession of some environments, especially those severely degraded ones (Génin et al., 2021). Hence, proper selection of a nurse plant can determine the success of a sustainable ecological restoration project.

One specific type of facilitation involving the interaction between adult plants and seedlings is known as ‘Nurse Plant Syndrome’. The nurse plant syndrome was originally coined by Niering et al. (1963) to describe plants that have positive ‘nursing’ effects on their own seedlings under their canopy compared to the gap spaces outside their canopy. This is positive spatial associations between seedlings of one plant, whether the same or of different species, to a sheltering adult plant (Steenbergh, 1977). Nurse Plants may buffer non-optimal environmental situations, which could be important in water-limited environments, by aiding in the interception of rainfall (Padilla and Pugnaire, 2006), improvement of abiotic stress conditions (Bertness and Callaway, 1994), poor starting conditions, and sluggish growth due to extreme temperatures (Flores and Jurado, 2003). It can create a shade consequently dropping thermal temperatures and reducing soil water evaporation (Domingo et al., 1999), the shade can also cut down radiations to help shield seedlings from the harmful effects of both extreme temperatures and low air moisture in arid environments (Pugnaire et al., 2011). Nurse plants could additionally reduce frost effect (Padilla and Pugnaire, 2006), act as windbreaks (Walker et al., 2007), increase seed arrival and trapping (Giladi et al., 2013), supply nutrients, and stock water (Flores and Jurado, 2003). Nurse plants may protect seedlings growing beneath them against grazing (Padilla and Pugnaire, 2006).

Regarding soils, a nurse plant can also positively modify soil nutrients (Walker et al., 2001), by accumulating litters and sediments, thus increasing nutrient content (Callaway, 1995), ultimately ameliorating the micro-climate when compared to nearby open areas (Pugnaire et al., 1996). It can also indirectly enhance soil chemistry for understory plants through mycorrhizal-colonization facilitation, with an upsurge in nutrient availability for such plants along with an increase in microbial abundance under nurse plants leading to higher mineralization and availability of nutrients (Moro et al., 1997) for beneficiaries leading to facilitation (Rodríguez-Echeverría et al., 2016). In 2014, Filazzola and Lortie (2014) reviewed 298 articles on nurse-plant interactions based on geographic region, mechanism of facilitation, ecological hypothesis, and nurse life-form. Results showed that the majority of studies of positive plant interactions were most frequent in areas of high abiotic stress especially in Arid and Semi-Arid climate (43.6 %).

Nurse plants were already tested for restoration in disturbed lands (Gómez-Aparicio, 2009) and extreme environments, with native species being one of the most appropriate choices. Nurse plants improve environmental conditions for seedling establishment by enhancing soil moisture and organic matter contents (Singh and Kumar, 2022; Leite et al., 2022). In arid (Arriaga et al., 1993), and semi-arid regions, almost a third of nurse plants are leguminous plants capable of fixing nitrogen through a symbiotic relationship with root-nodulating bacteria (Flores and Jurado, 2003). Leading to an improvement in soil nutrient content (den Hollander et al., 2007) and an enhancement in soil nitrogen availability (Barnes and Archer, 1996). This characteristic is very important in Mediterranean soils, having nitrogen as a chronically

scarce nutrient (Alpert and Mooney, 1996). Therefore, leguminous species can be good candidates for being potential nurse species for Mediterranean soil and herbaceous plant community restoration.

Subterranean clover (*Trifolium subterraneum* L.) has been considered as a theoretical foundation species capable of restoring nitrogen-depleted fields. *T. subterraneum* is native to the Mediterranean Basin, West Asia, and the Atlantic coast of Western Europe (San Miguel, 2008), growing on dry soils of open plains and mountains, ranging from sea level up to an altitude of 1800 m (Ecocrop, 2017). Native to Lebanon (Tohmé and Tohmé, 2014), it is a multi-stemmed therophytic species, flowering in March–April, and setting fruits in April–May (Vasileva et al., 2016). Several calyces of the upper-most sterile flowers form a drilling apparatus allowing the formed heads to penetrate the soil (geocarp) (Falistocco et al., 1987), transforming into a buried pod. *T. subterraneum* has high ecological flexibility, with habitat ranging from sparse oak forests to pastures, with soil covering properties and nitrification qualities (Vasileva et al., 2016). It is a versatile plant already used for weed suppression (because of size and spread), green manure (producing 112 to 224 kg N/ha), mulching substance (dry mulch in late spring and green mulch in fall), grazing (being very palatable), Nitrogen fixing (Clark, 2007), and erosion control (Howieson et al., 2000). Other desirable qualities include an annual life cycle coinciding with the abundant rainfall (from autumn to spring), tolerance of regular and close grazing (due to prostrate growth habit), and natural regeneration through reducing the need for re-seeding, hence protecting its seeds from being eaten by stock (Nichols et al., 1994). As a legume species, *T. subterraneum* is a nitrogen-fixing plant (Ferreira and Castro, 2005) coexisting with vesicular-arbuscular mycorrhizas (VAM) or with *Rhizobium leguminosarum* biovar *trifolii* bacteria species, allowing it to fix about 50 to 188 kg/ha of nitrogen per year (Bolger et al., 1995).

Nevertheless, species interactions, including competitive or facilitative abilities, depend on disturbances or abiotic constraints and are principally driven by soil resources (Liancourt et al., 2009). This balance between competition and facilitation interactions can develop according to species involved and the presence of abiotic filters such as soil properties (Rajaniemi and Allison, 2009). To assess such processes, mesocosm experiments involving interspecific interactions appear to be an appropriate approach, as already suggested by Fraser and Keddy (1997) and Hager (2004). However, few works have proposed splitting plant facilitative and/or competitive effects and responses simultaneously. This initial step could enable the identification of potential nurse plants in semi-controlled ex-situ interspecific interaction experiments for utilizing nurse species effects for restoring soil fertility of degraded areas directly in the field.

Aims were to comprehend different interactions between a potential native nurse plant (*T. subterraneum*) and four naturally co-existing species (*Aegilops triuncialis* L., *Echinops viscosus* L., *Eryngium creticum* Lam., *Hyoscyamus aureus* L.) all found in the Mediterranean grasslands of Lebanon. It was also a question of determining all the possible influences on plant interactions of the physico-chemical characteristics of pre-existing soils, degraded and non-degraded, with or without incorporation of organic matter produced by *T. subterraneum* itself.

The detailed objectives were for soils (1), to test the impacts of soil degradation by quarry exploitation on physico-chemical soil properties for reference and degraded ecosystems before the improvement by sowing *T. subterraneum* as a potential nurse species (2), to test the impacts of one year *T. subterraneum* cultivation on degraded and reference soils without addition of dried *T. subterraneum* biomass in the soil (3), to test the impacts of two years *T. subterraneum* cultivation on degraded and reference soils with addition of dried *T. subterraneum* biomass in the soil. For plants (1), to test the effects of *T. subterraneum* on target plant biomass (RIeffect) without addition of dried *T. subterraneum* biomass and (2), with addition of dried *T. subterraneum* biomass. At least (3), we test the effects of *T. subterraneum* and soil improvement of degraded soil on *T. subterraneum* biomass itself.

Our main hypotheses were that the cultivation of *T. subterraneum*

would promote facilitating relationships with other target species, particularly after incorporation of its dry biomass after one year of cultivation due to a significant increase in soil fertility, particularly that from the degraded site.

2. Materials and methods

2.1. Target species selected for the ex situ experiment

Four native species were selected: *A. triuncialis*., *E. viscosus*, *E. creticum*, and *H. aureus*, chosen for the experiment because of their abundance in the reference ecosystem and Lebanon's dry Mediterranean grasslands, their suitability as target plants for restoring Mediterranean grasslands in Lebanon following any degradation (such as quarry exploitation) and the fact that their seeds exhibit high germination rates.

2.2. Soil collection in the field before the ex situ experiment

Soil samples needed for the experiment were extracted from a quarry

(degraded site) located in the vicinity of Maqneh (34.0787° N, 36.2095° E) in the eastern Beqaa plain, Lebanon. The reference soil samples were extracted from the nearby Mediterranean dry grassland (reference ecosystem). A total soil volume of 14 m³ (7 m³ from both the reference ecosystem and the degraded quarry) was collected from the top 10 cm layer. It was then transported to the experimental ex-situ site, a south-facing, 200-µm sheathed tunnel greenhouse at an altitude of 700 m.a.s.l. in Zahrieh (33.8920° N, 35.6758° E) near Beyrouth.

2.3. Seed collection in the field before the ex situ experiment

The seeds of the four-target species were hand-harvested at the conclusion of the flowering season within a 0.5 km radius of the quarry in September 2017. Subsequently, they were air-dried in the shade, threshed, cleaned, and stored in tightly sealed plastic boxes treated with the sphere-shaped fumigant insecticide Naphthalene (C₁₀H₈) to eradicate any potential larvae or adult insects. Seeds of *T. subterraneum* were obtained from the Fertiprado Company (France) corresponding to a variety adapted for semi-arid areas.

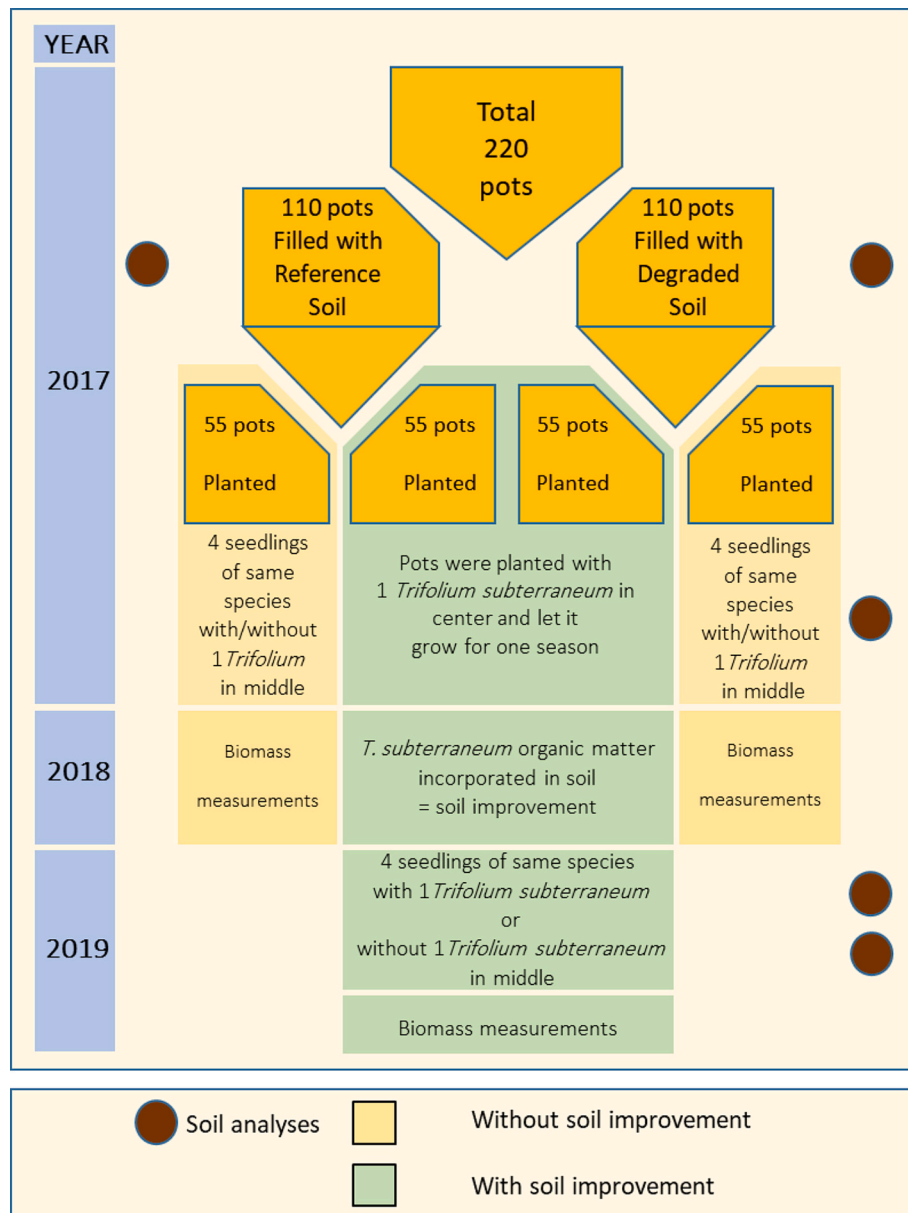


Fig. 1. Schematic representation of the experimental design of the ex situ experiment for the 3-year period.

2.4. Experimental design and procedure of the ex situ experiment

Although the experiment is a continuous study, it could be divided into three phases, spanning from 2017 to 2019.

These phases encompass:

- A preparation phase (2017), where required seeds and soils were collected (for testing and analysis at set-up time and for the experiment in the greenhouse). The soil result analysis performed at this phase will be referred to in the manuscript as “at set-up time”.
- An experiment (2018), to evaluate the effect of *T. subterraneum* on target species in both degraded and reference soils, without addition of dried *T. subterraneum* biomass. The data collected and analyzed in this context will be denoted as “without improvement” in the manuscript.
- An experiment to evaluate the effect of *T. subterraneum* on target species on both the degraded and reference soils after addition of dried *T. subterraneum* biomass. To achieve this, *T. subterraneum* was grown independently for one year in pots of both degraded and reference soils. Following its demise, the dry biomass of *T. subterraneum* was incorporated into both soil types. Subsequently, the previous one-year experiment was repeated to evaluate the effect of *T. subterraneum* on target species in 2019. The data collected and analyzed in this context will be labeled as “with improvement” in the manuscript.

In total, 220 pots were divided equally into 110 pots filled with soil from the reference ecosystem and 110 pots from the degraded ecosystem. All the pots (110 pots of both soil types) were further separated into 55 pots for the first-year experiment in 2018 and 55 pots for the second-year experiment in 2019 (Fig. 1).

2.5. Soil preparation for pots using during the ex situ experiment

The soil used in the experiment was sieved through a 2-mm sieve mesh, mixed with perlite (an inert material used to ventilate, loosen, and increase soil drainage) at a ratio of 10:1, and filled in 22.5 cm-diameter (5-l pots). A 3 cm layer of pebbles (size 0.5–1 cm) was placed at the bottom of each pot before adding soil for drainage. A 2 mm-thick geotextile fabric separated the bottom pebble layer from the soil, preventing soil loss and permitting appropriate water drainage.

2.6. Soil analyses before and during the ex situ experiment

To test soil characteristics at set-up time, five soil samples from both sites (the reference and degraded ecosystem), each weighing 100 g, were randomly selected, dried, sieved through a 2-mm mesh sieve, and tested for various physical and chemical properties at Teyssier Laboratory (Bordeaux, France). Soil analyses were also run on degraded soils from the pots without addition of *T. subterraneum* biomass after one year of *T. subterraneum* grown with its targets ($N = 5$), and on degraded soils from pots with soil improvement ($N = 5$), after one year of *T. subterraneum* being grown alone and incorporated into the soil ($N = 5$) and the second year of *T. subterraneum* grown with its targets ($N = 5$). The performed soil analysis covered the following parameters: pH water ratio 1:5, CaCO_3 using a Bernard Calcimeter, organic C, Total N by dry combustion, C:N ratio, Cation Exchange Capacity (CEC), exchangeable K^+ , plant-available P, and the particle-size distribution in 5 fractions without prior decarbonation (clay- less than 0.002 mm, fine silt- between 0.002 and 0.02 mm, coarse silt- between 0.02 and 0.2 mm, fine sand- between 0.05 and 0.2 mm, and coarse sand- between 0.2 and 2 mm). These soil variables were chosen because there are standardised good indicators of agronomical soil fertility measurements (total N, organic C, C:N, CEC, plant-available-P, pH, etc.) and they are directly related to plant biomass which is the best predictor of competition ability when using Relative Interaction Intensity Index (RII) (see below).

2.7. Performed ex situ experiments in microcosms

To avoid any potential failures during the early seedling growth

phase and minimize weed competition from the soil seed bank, all seeds were initially germinated in plastic trays at the onset of the experiment. Germination was conducted in a controlled environment within a germination chamber, maintaining a temperature of 22/24 °C and a night/day light cycle of 08/16 h. The germination medium comprised a 2:1 ratio mixture, combining two parts soil from either a reference or degraded ecosystem with one part regular commercial seed-germination medium. Once the seedlings developed beyond the cotyledon phase into the first set of true leaves, they were placed under a 50 % shade net for three days, allowing them to harden and acclimatise to fluctuating day and night temperatures and to adapt to direct sunlight under greenhouse conditions gradually. Finally, they were all transplanted into the intended pots. Pots, spaced at an inter / intra-row distance of 20 cm, were placed on a concrete floor to eliminate any emerging voluntary weeds. Each pot was equipped with an individual online dripper in a drip irrigation system. Prior to planting but after soil filling, all pots received thorough watering for two weeks. This facilitated the removal of any germinated spontaneous weeds with minimal soil disturbance.

The experiment followed the competition protocol suggested by Gaudet and Keddy (1988, 1995). In the first group of pots (Fig. 2a), the potential nurse plant, *T. subterraneum*, was planted alone in the middle. In a second group, *T. subterraneum* was planted in the middle of each pot with four seedlings of the same species transplanted equidistantly in each pot (5 plants in total) (Fig. 2b). In the third group (Fig. 2c), *T. subterraneum* was omitted. Finally, in the last group of pots, the potential nurse plant *T. subterraneum* was planted in the middle along with four seedlings of *T. subterraneum* (Fig. 2d). All of the above treatments were replicated five times.

The second set of pots (110 pots) was split evenly into two groups (55 in each), filled with soil from either the reference or degraded ecosystems. All pots were planted with a single seedling of *T. subterraneum* in the center (Fig. 1) and allowed to grow through its complete lifecycle, including the seedling stage, vegetative growth, inflorescences, seed set, and eventual decline. After seven months, the dried *T. subterraneum* plant material was harvested, chopped into 2–3 cm fragments, re-incorporated in the soil, and set aside for five months until the subsequent growing season. At the beginning of the following growing season, the exact procedure from the first season was meticulously reapplied, replicating all planting combinations five times (Fig. 1).

2.8. Plant treat measurements during the ex situ experiment

The performance of both *T. subterraneum* and the target species was assessed in early summer, corresponding to the phenological stage of the beginning of fructification of the target species and before the completion of the life cycle of annual species in late summer. The functional trait measured was the total above-ground biomass of the vegetative parts and seed. This involved cutting the vegetative parts at the soil level, placing them in individually coded paper bags, and subsequently oven-drying at 50 °C for 48 h. Finally, the weighed plant samples from the bags were recorded.

Data collected from the interaction between *T. subterraneum* and target plants was assessed by applying the Relative Interaction Intensity Index (RII) to plant biomass. RII was the tool chosen to evaluate the interaction because of the following mathematical and statistical properties: (1) It is symmetrical in relation to zero, with identical absolute values for competition and facilitation (from −1 to 0 indicates competition and from 0 to +1 indicates facilitation), (2) It is linear, and (3) It has no discontinuity within its range (Liancourt et al., 2009).

RIIs were calculated according to the following equation:

$$RII_{\text{effect}} = \frac{(\text{Biomass}_{\text{NwithTrifolium}} - \text{Biomass}_{\text{NwithoutTrifolium}})}{(\text{Biomass}_{\text{NwithTrifolium}} + \text{Biomass}_{\text{NwithoutTrifolium}})}$$

Where biomass is measured on $N =$ the average biomass of four targets of one species (*A. triuncialis*, *E. viscosus*, *Er. creticum*, *H. aureus*, or *T. subterraneum*), biomass was measured in the presence or absence of

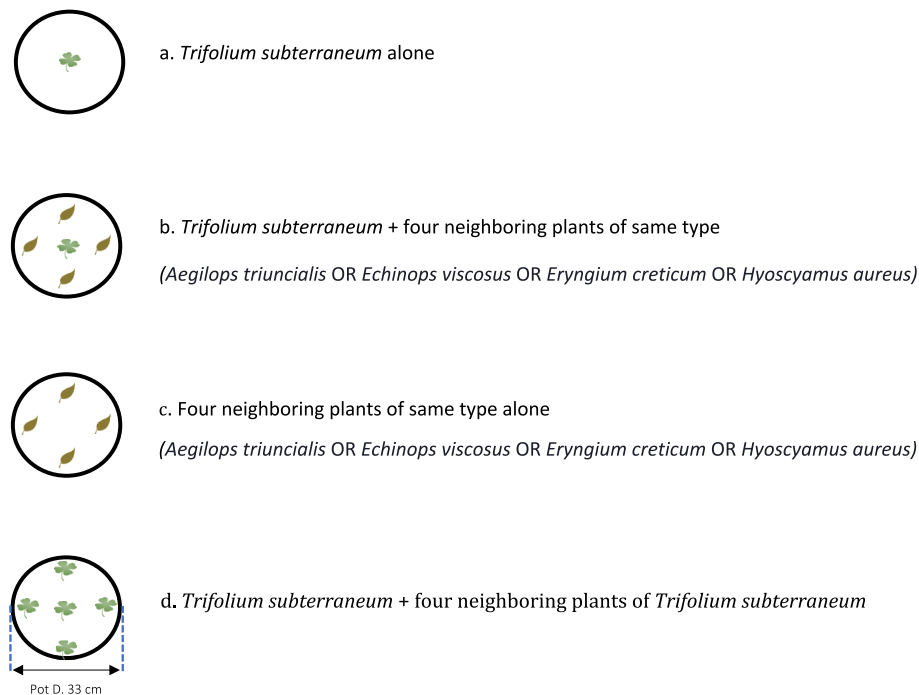


Fig. 2. Experimental design, plant arrangements in pots of the ex situ experiment for the 3-year period.

the potential nurse plant *T. subterraneum*. As there were four individuals of each target species/pot, their average biomass was considered.

2.9. Statistical analyses

All analyses were performed with R-3.6.0 (R Core Team, 2022). Prior to applying statistical analysis, data distributions were examined using the Shapiro–Wilk test of normality and homogeneity of variance was tested with the Levene's Test.

2.9.1. Soil statistical analyses

Generalized Linear Models (GLMs) were fitted to investigate the effects of the different treatments applied in the pots on soil physico-chemical variables (response variables). GLMs with Gaussian distribution (link = “identity”) were fitted when residuals were normally distributed, and GLMs with gamma distribution (link = “inverse”) were applied when residuals did not comply with the assumption of a normal distribution.

Models were followed by Tukey HSD post-hoc tests using the glht function with $P < 0.05$ from the “multcomp” package (Hothorn et al., 2016).

2.9.2. Plant data statistical analyses

To assess the competitive effect of *T. subterraneum* (ability to reduce the performance of target species), two-way ANOVAs (package “stats”) or two-way ART ANOVAs (Aligned Ranks Transformation ANOVAs; package “ARTool”) were performed on the RII_{effect} (response variables) respectively, without soil improvement and with soil improvement. The interaction of two explanatory variables was tested for (1) the type of soil (reference vs. degraded) and (2) the identity of the target species. ANOVAs were applied when data responded to the assumptions of normality and homogeneity of variance (package “nortest”, Lilliefors test and package “car”, Levene test). ART ANOVAs were performed when otherwise (Mangiafico, 2016). All were followed by pairwise contrast comparisons with a Tukey adjustment when significant (“emmeans” and “multcomp” packages). In order to find out if each RII was significant from zero, thus indicating competition or facilitation, a Wilcoxon test (package “stats”) was performed on each level of

explanatory variables.

To study the effect of *T. subterraneum* as a nurse plant, Generalized Linear Models (GLM) were fitted with a Gamma distribution (link = “inverse”) on *T. subterraneum* biomass (response variable) grown only on degraded soils (package “stats”). The interaction of two explanatory variables was tested (1) in the presence of *T. subterraneum* as a nurse plant and (2) whether degraded soil was improved or not. All models were followed by pairwise contrast comparisons with a Tukey adjustment when significant (“emmeans” and “multcomp” packages).

3. Results

3.1. Soil results

3.1.1. Comparison of soil properties for reference and degraded ecosystems (at set-up time)

In 2017, before initiating the experiment, soil collected from the degraded ecosystem had significantly higher clay contents compared to the grassland reference ecosystem (Table 1). On the opposite hand, fine sand and coarse sand contents were significantly lower in the degraded ecosystem (Table 1). Significantly higher CEC was also measured in degraded soil in comparison with the reference soil. Degraded soil also showed a significantly higher water-pH and pH-KCL than the reference soil (Table 2). Nevertheless, total nitrogen (Fig. 3), carbon (Fig. 4), and available phosphorus (Fig. 5) were significantly lower in degraded soil than in the reference soil. Total Ca, K, CaO, and C:N ratios were not significantly different between the two soil types in 2017 (Table 2).

3.1.2. Comparison of soil properties of degraded soil at set-up time vs. degraded soil with no addition of dried *T. subterraneum* biomass

Although *T. subterraneum* and target species grown for several months only, there was a significant increase in available phosphorus levels between the initial degraded soil of 2017 and 2018 after *T. subterraneum* and target species cultivation (Fig. 5). Also, CaO and NaO increased significantly between the degraded soil at set-up time and in degraded soil without improvement (Table 2). Another noteworthy figure was a significant reduction in potassium contents when comparing its levels between the degraded soil at set-up time and in

Table 1

Results of physical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up (2017), and with the different treatments applied in the pots to the degraded soil without soil improvement (2018). TS is *T. subterraneum*. Values are means $\pm$ standard errors. Significant differences according to ANOVA and Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

Soil Type	df	F	P-value	Reference soil at time of set-up 2017	Reference soil without soil improvement – TS 2018	Degraded soil at time of set-up 2017	Degraded soil without soil improvement – TS 2018
Clay (g/Kg soil)	3	36.44	< 0.001	209.6 $\pm$ 9.8 ^a	246.6 $\pm$ 8.2 ^b	251.2 $\pm$ 14.6 ^b	330.6 $\pm$ 3.0 ^c
Fine Silt (g/Kg soil)	3	1.18	0.35	324.4 $\pm$ 5.0 ^a	364.8 $\pm$ 4.0 ^a	388.2 $\pm$ 12.7 ^a	305.6 $\pm$ 67.1 ^a
Coarse Silt (g/Kg soil)	3	40.39	< 0.001	117.4 $\pm$ 2.7 ^a	81.4 $\pm$ 3.8 ^b	116.7 $\pm$ 4.9 ^a	66.5 $\pm$ 2.7 ^b
Fine Sand (g/Kg soil)	3	52.80	< 0.001	145.0 $\pm$ 5.5 ^a	121.6 $\pm$ 5.1 ^b	101.0 $\pm$ 5.2 ^c	81.4 $\pm$ 0.8 ^c
Coarse Sand (g/Kg soil)	3	39.10	< 0.001	203.8 $\pm$ 7.7 ^a	185.6 $\pm$ 6.5 ^a	143.2 $\pm$ 17.4 ^b	149.4 $\pm$ 3.7 ^c

Table 2

Results of chemical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up (2017), with the different treatments applied in the pots to the degraded soil without soil improvement (2018), and after soil improvement (2019). TS is *T. subterraneum*- TR is Target plants. Values are means $\pm$ standard errors. Significant differences according to ANOVA and Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

Soil Tests Performed	df	F	P-value	Degraded soil at time of set-up 2017	Degraded Soil without soil improvement + TS 2018	Degraded Soil with soil improvement + TS 2019	Degraded Soil with soil improvement + TS + TR 2019	Reference soil at time of set-up 2017
CEC (meq/100gsoil)	4	19.8	<0.001	14.7 $\pm$ 0.5 ^a	13.8 $\pm$ 0.3 ^a	11.5 $\pm$ 0.4 ^b	11.5 $\pm$ 0.5 ^b	12.16 $\pm$ 0.2 ^b
pH Water	4	51.6	<0.001	8.6 $\pm$ 0.03 ^a	8.3 $\pm$ 0.05 ^b	8 $\pm$ 0.03 ^c	8.1 $\pm$ 0.03 ^c	8.4 $\pm$ 0.02 ^b
pH KCl	4	4.4	0.01	7.8 $\pm$ 0.02 ^a	7.8 $\pm$ 0.02 ^a	7.8 $\pm$ 0 ^{ab}	7.8 $\pm$ 0 ^{ab}	7.74 $\pm$ 0.02 ^b
CaCO ₃	4	11	<0.001	68.2 $\pm$ 0.4 ^a	72.2 $\pm$ 0.5 ^a	51.4 $\pm$ 4.7 ^b	69.4 $\pm$ 0.7 ^a	71.4 $\pm$ 0.4 ^a
P ₂ O ₅ Olsen (mg/Kg Soil)	4	83.9	<0.001	34.8 $\pm$ 0.4 ^a	42.8 $\pm$ 1.4 ^b	50.2 $\pm$ 1.5 ^c	45.6 $\pm$ 0.2 ^b	58.6 $\pm$ 0.4 ^d
K ₂ O (mg/Kg Soil)	4	28.3	<0.001	300.2 $\pm$ 4.6 ^a	192.2 $\pm$ 20.8 ^{bc}	221.4 $\pm$ 5.7 ^c	166.8 $\pm$ 1.4 ^b	313.6 $\pm$ 7.7 ^a
MgO (mg/Kg Soil)	4	99.8	<0.001	461.6 $\pm$ 9.1 ^{ab}	440.8 $\pm$ 8.8 ^a	468.2 $\pm$ 5.3 ^b	448.8 $\pm$ 1.4 ^{ab}	325 $\pm$ 4.1 ^c
CaO (mg/Kg Soil)	4	15.4	<0.001	11,140 $\pm$ 80.5 ^a	9991.2 $\pm$ 216.1 ^b	10,999.8 $\pm$ 56.3 ^a	10,828 $\pm$ 26 ^a	10,962 $\pm$ 79.1 ^a
Na ₂ O (mg/Kg Soil)	4	198.3	<0.001	21.8 $\pm$ 0.4 ^a	90.4 $\pm$ 14.4 ^b	231.6 $\pm$ 9.2 ^c	192.4 $\pm$ 3.2 ^c	18 $\pm$ 0.8 ^a
N total (mg/Kg Soil)	4	52.5	<0.001	560 $\pm$ 4 ^a	559.6 $\pm$ 36.8 ^a	692 $\pm$ 36.9 ^b	659.4 $\pm$ 26.4 ^{ab}	1068.2 $\pm$ 27.7 ^c
Carbon (mg/Kg Soil)	4	20.5	<0.001	4.6 $\pm$ 0.1 ^a	5.0 $\pm$ 0.09 ^a	8 $\pm$ 0.7 ^{bc}	7 $\pm$ 0.8 ^b	9.5 $\pm$ 0.2 ^c
C:N ratio	4	4.7	0.008	8.3 $\pm$ 0.2 ^a	9.1 $\pm$ 0.7 ^{ab}	11.6 $\pm$ 0.8 ^b	10.5 $\pm$ 0.8 ^{ab}	8.9 $\pm$ 0.4 ^a

degraded soil without improvement (Fig. 6).

3.1.3. Comparison of soil properties of degraded soil at set-up time vs. degraded soil after addition of dried *T. subterraneum* biomass

A significant decrease in CEC (Table 2) was measured in improved soils compared with the degraded soil at set-up time. On the opposite, Carbon increased significantly with soil improvement (Fig. 4). However, it is worth noting that after improvement, C amounts were still significantly below those in the reference soil (Fig. 4). Total soil nitrogen was significantly higher in degraded soil with improvement than in degraded soil at set-up time when *T. subterraneum* was grown alone, and marginally significant when *T. subterraneum* and target plants were grown together. Still, it is worth noting that the nitrogen level was also still significantly higher in the reference soil (Fig. 3).

Available phosphorus significantly increased between degraded soil at set-up time and all degraded soils with a treatment. Nevertheless, it is worth mentioning that the phosphorus content of the degraded soils did not also reach the phosphorus content of the reference soil (Fig. 5).

3.2. Results for plants

3.2.1. Effect of *T. Subterraneum* on target plant biomass (R_{II}^{effect}) without addition of dried *T. subterraneum* biomass

There was no significant soil effect (degraded vs. reference) on target species RII indices without soil improvement ($F = 0.61$, $p = 0.439$) nor significant interactions between explanatory variables (soil $\times$ species; $F = 1.20$, $p = 0.327$). On the other hand, *T. subterraneum* competed slightly against all species (none of these RII were significant from zero) but had a significant facilitative effect on itself (RII significantly different from zero; $V = 54$, $p = 0.004^{**}$; Fig. 7). Only the competition with *Eryngium* was significantly different from facilitation with itself (Fig. 7; $F = 2.89$, $p = 0.034^{*}$).

3.2.2. Effect of *T. On target plant biomass (R_{II}^{effect}) after addition of dried *T. subterraneum* biomass*

After soil improvement, there was a significant effect of soil on target species RII ($F = 8.30$, $p = 0.006^{**}$; Fig. 8): target species RII was lower on improved degraded soil than on improved reference soil, indicating that *T. subterraneum* competition was greater on improved degraded soil. Moreover, the RII on improved degraded soil is significantly different

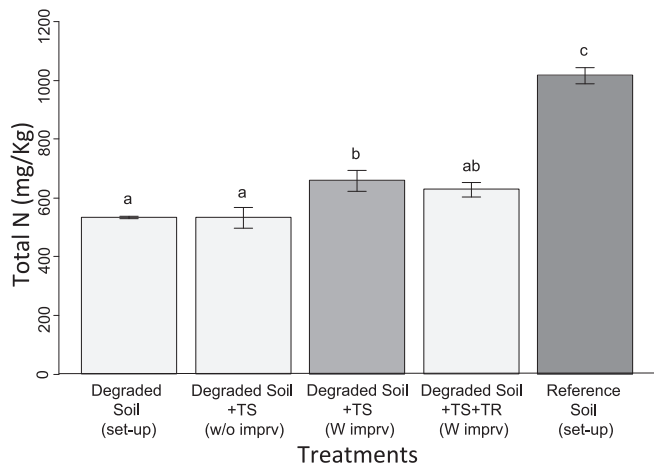


Fig. 3. Total Nitrogen contents measured in-situ degraded soil at the time of set-up (2017) and with the different treatments applied in the pots to the degraded soil without soil improvement (2018) and with soil improvement (2019) ($F = 52.5$, $P < 0.001$). TS is *T. subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “W imprv” is with soil improvement. Values are means $\pm$ standard errors. Significant differences according to Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

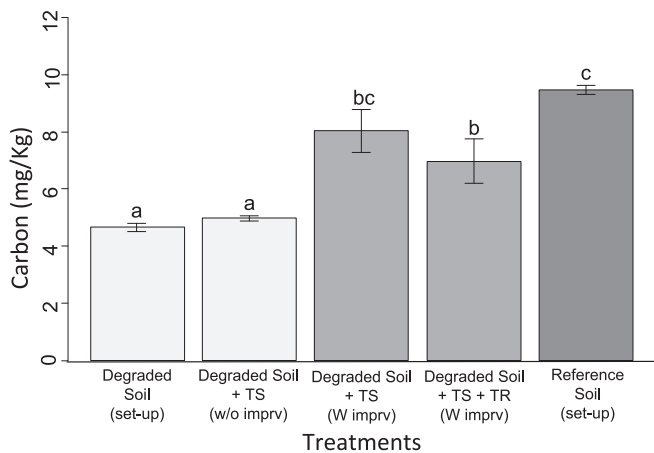


Fig. 4. Soil Carbon analyses performed for in-situ degraded soil and reference soil at the time of set-up (2017) and with the different treatments applied in the pots to the degraded soil without soil improvement (2018) and with soil improvement (2019) ($F = 20.5$, $P < 0.001$). TS is *T. subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “W imprv” is with soil improvement. Values are means $\pm$ standard errors. Significant differences according to Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

from zero ($V = 60$, $p = 0.006^{**}$; Fig. 8). There were also significant differences in the target species RII ($F = 12.65$, $p < 0.001^{***}$; Fig. 9): *T. subterraneum* competed against all species but itself, and *E. viscosus* and *H. aureus* RII were significantly different from zero ($V = 0$, $p = 0.002^{**}$ and $V = 6$, $p = 0.027^{*}$ respectively). *T. subterraneum* has a significant facilitative effect on itself, as the RII is significantly different from zero ($V = 50$, $p = 0.020^{*}$; Fig. 9).

3.2.3. Effect of *T. subterraneum* and soil improvement of degraded soil on *T. subterraneum* biomass

We found no significant positive effect of the improvement of degraded soil by *T. subterraneum* on *T. subterraneum* biomass (i.e., biomass after soil improvement was not significantly higher than before

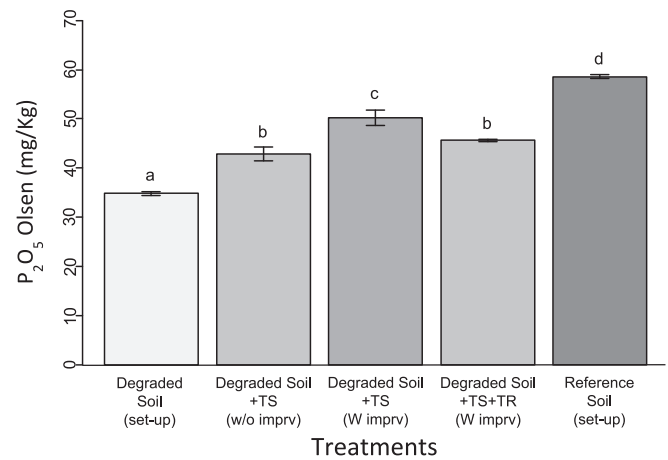


Fig. 5. Available Phosphorus contents measured in-situ degraded soil and reference soil at the time of set-up (2018) and with the different treatments applied in the pots to the degraded soil without soil improvement (2018) and with soil improvement (2019) ($F = 83.9$, $P < 0.001$). TS is *T. subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “W imprv” is with soil improvement. Values are means $\pm$ standard errors. Significant differences according to Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

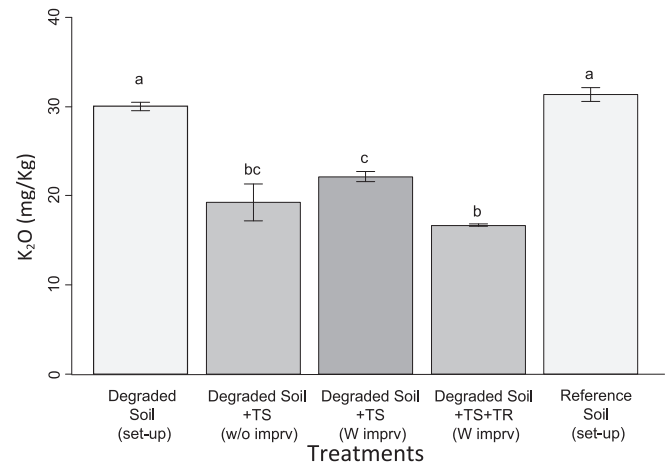


Fig. 6. Potassium contents measured in-situ degraded soil and reference soil at the time of set-up (2017), and the different treatments applied in the pots to the degraded soil without soil improvement (2018) and later after soil improvement (2019) ($F = 28.3$, $P < 0.001$). TS is *T. subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “W imprv” is with soil improvement. Values are means $\pm$ standard errors. Significant differences according to Tukey post hoc tests are indicated by different letters. The significance thresholds have been set at a 5 % risk ($p < 0.05$).

soil improvement) (Fig. 10; $X^2 = 0.67$, $p = 0.511$). *T. subterraneum* had a significant facilitative effect on itself (Fig. 10; $X^2 = 0.30$, $p < 0.001$).

4. Discussion

Our study, performed under ex-situ conditions, promoted more comprehension of plant-plant interactions. Such interactions are associated with plant communities in semiarid Mediterranean grasslands, with the possible use of native plants as nurse plants to aid in the rehabilitation of degraded systems (Singh and Kumar, 2022; Saby et al., 2024). The outcome from this semi-controlled interspecific interaction experiment indicated that with *T. subterraneum* used as a nurse plant, competition rather than facilitation dominated the interactions amongst

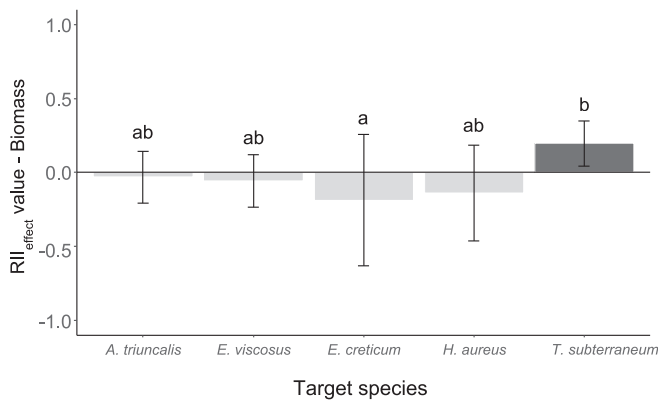


Fig. 7. Effect of *T. subterraneum* on target species biomass depending on target species identity without soil improvement ($F = 2.89$, $p = 0.034^*$): mean RII effect per replicate pot ($N = 5$). The horizontal line marks $RII = 0$, above which positive RII values indicate facilitation and below which negative values indicate competition. Species sharing a letter were not significantly different from each other ($p < 0.05$). Box-plots colored dark gray show RII significantly different from 0 (tested by Wilcoxon test).

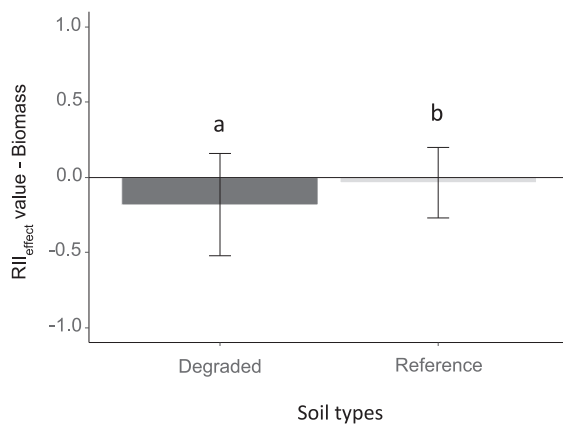


Fig. 8. Effect of *T. subterraneum* on target species biomass depending on soil type after soil improvement ($F = 8.30$, $p = 0.006^{**}$). Mean RII effect per replicate pot ($N = 5$). The horizontal line marks $RII = 0$, above which positive RII values indicate facilitation and below which negative values indicate competition. Soil types sharing a different letter were significantly different from each other ($p < 0.05$). Box-plots colored dark gray show RII significantly different from 0 (tested by Wilcoxon test).

the studied plant species. Such results could also provide diverse ways and means that might aid in detecting potential nurse plant species or structuring species capable of increasing the successional dynamics of a plant community. Although ex-situ studies cannot substitute in-situ experimentations (Forero et al., 2019), they could be the first step in selecting different designs, management methods, and various species needed to utilize in any ecological restoration procedure with less costly in-situ settings.

4.1. Impacts of *T. subterraneum* on soil physico-chemical properties

Before initiating the experiment in 2017, soils tested from the reference and degraded plots revealed several significant differences in physical and chemical properties due to the impacts of the quarry exploitation on the dry grassland soil upper-layers (removal by extraction or erosion in the slopes surrounding the quarry).

The significant increase of total Carbon and total N was evident in degraded soils between 2017 and 2019 for *T. subterraneum* cultivated alone and marginally significant for *T. subterraneum* + target plants.

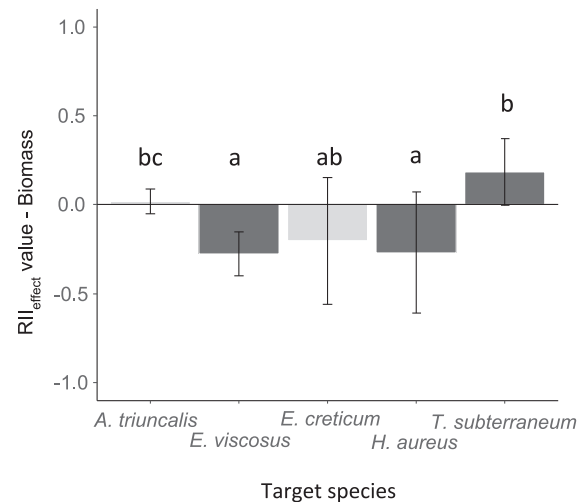


Fig. 9. Effect of *T. subterraneum* on target species biomass depending on target species identity after soil improvement ($F = 12.65$, $p < 0.001^{***}$). Mean RII effect per replicate pot ($N = 5$). The horizontal line marks $RII = 0$, above which the positive RII values indicate facilitation, and below which the negative RII values indicate competition. Species sharing a letter were not significantly different from each other ($p < 0.05$). Box-plots colored dark gray show RII significantly different from 0 (Tested by Wilcoxon test).

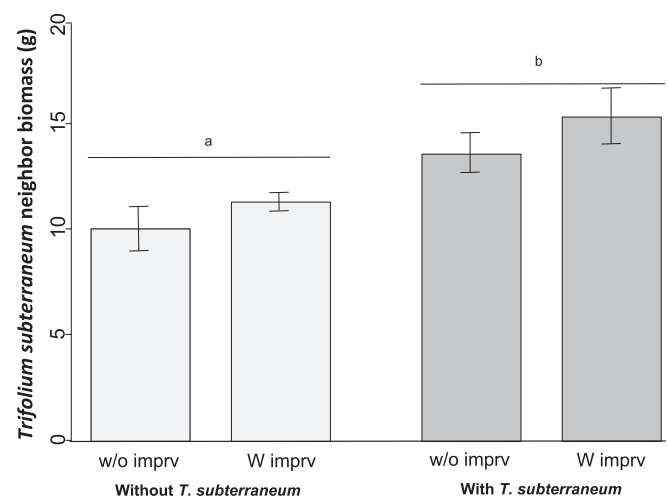


Fig. 10. Effect of *T. subterraneum* as a nurse plant and soil improvement on target *T. subterraneum* biomass grown on degraded soils ($X^2 = 0.30$, $p < 0.001$, $N = 5$). Bars sharing a letter were not significantly different from each other ($p < 0.05$). “w/o imprv” is without soil improvement- “W imprv” is with soil improvement. Without *T. subterraneum* = Without *T. subterraneum* as a nurse plant; With *T. subterraneum* = With *T. subterraneum* as a nurse plant.

Still, it is worth noting that after two growing seasons (even with the incorporation of *T. subterraneum*), degraded soil total C and total N remained unfortunately in a restoration perspective below that of total C and total N from the initial soil collected from the reference dry grassland site in 2017.

Significant differences were also evident between P_2O_5 in degraded and the reference dry grassland soil in 2017. This difference could be due because phosphorus does not readily leach out of the root zone and is potentially only lost by erosion and runoff. A significant increase in available Phosphorus was evident in 2018, possibly due to the degradation of total phosphorus into available phosphorus from the soil minerals under root actions that emit weak acids (Vet et al., 2014). An increase in OM is also a relevant factor in controlling Phosphorus availability. The addition of OM (via dry material incorporation) leads

to organic P mineralization through the exudation of organic acids or phosphatase enzymes by plant roots or Mycorrhiza (Jones and Darrah, 1994). This mineralization of OM tends to provide a significant portion of the required P needed for the plants. A significant increase in P_2O_5 was also noticeable within degraded soils between 2017 and 2019 in *T. subterraneum* alone and *T. subterraneum* + target plants. Still, it is worth mentioning again that the P level in degraded soil unfortunately did not attain the level of the reference dry grassland soil.

At the opposite, a significant reduction was noted for K_2O when comparing the degraded soil collected in 2017, after one growing season (2018) and in 2019 even with the incorporation of *T. subterraneum* OM in the soils. This fact might be attributed to the high tendency of *T. subterraneum* to absorb K_2O from the soil (Barrow, 1966), an act amplified in pots, where the lost of K and others cations (as revealed by the significant decrease of the CEC) may be due to the absorption of the cations by the plants and losses by leaching following watering, with no possible replacement being an experiment designed in pots without fertilizer applications.

At least, NaO increased significantly between the degraded soils from 2017 to 2019. In excess, Na can degrade soil structure, slow infiltration rates, and interfere with Ca, Mg, and K uptake (Hodges, 2010). Nevertheless, this increase in Na level could be a bias attributed to salt accumulations increasing gradually in the irrigation water after being pumped directly from the artesian. This bias was reduced between 2018 and 2019 by initially storing the water drawn from the artesian well in a new separate tank, leaving it to settle before irrigating the plants when needed.

To conclude, *T. subterraneum* is a Lebanon native species that seemed suitable to raise the C and N stocks in the redevelopment soil of abandoned quarries. However, these concentrations were still considerably lower than those measured in natural Mediterranean dry grasslands that preexisted before quarry exploitation even after incorporation of dry leaves, stems and roots of *T. subterraneum* into the degraded soil.

4.2. Impacts of *T. subterraneum* on interactions with target plants

Results of this experiment confirmed that *T. subterraneum* had a competitive effect, which in some situations is a major driving factor structuring plant communities, rather than a facilitative effect on the various target plants tested (Navas and Moreau-Richard, 2005). That was evident through the obtained measurements that revealed a significant reduction in plant heights, total above-ground biomass, and a lesser surface area for most target groups in both reference and degraded environments whatever the year (2018 or 2019) or the soil tested (degraded or reference soil).

Although several studies in literature highlighted the importance of nurse plants as facilitators in plant communities (Pugnaire et al., 2011), especially in harsh environmental conditions (Verdú and García-Fayos, 2003), our results align with previous studies in the Mediterranean ecosystems (Génin et al., 2021), highlighting the fact that competition, not facilitation, was the end result of the investigated plant interaction with or without changes in soil fertility resulting from the incorporation of *T. subterraneum* OM in soils between 2018 and 2019.

Nevertheless, our results clearly show that even at low nutrient levels in the degraded soil, the *T. subterranean* - like almost all nitrogen-fixing plants flourished, utilizing more efficiently required elements (especially N). This factor was reflected in better vegetative growth, accumulating more biomass, and size increase when compared to the target plants (that have no Nitrogen-fixing capabilities), ultimately succumbing to the competition. *T. subterraneum* exhibited only facilitation effects on biomass and surface cover when cultivated as a pure stand and incorporated as dry OM into the soil (2019). As for the effect of neighboring plants on *T. subterraneum*, it's apparent that the biomass of *T. subterraneum*, as a phytometer, was better on degraded soils in year 1 (2018) without target plants (with no significant species or interaction effect). In the second year (2019), probably due to the improvement of

the degraded soil, barely any difference was measured between degraded and reference treatments.

To conclude, only facilitation interactions were found when *T. subterraneum* was used as a pure stand and incorporated as dry OM into the soil.

4.3. Consequences for soil and Mediterranean dry grasslands restoration with the use of *T. subterraneum*

Hence, in a restoration perspective, *T. subterraneum* could be endorsed as an earlier introduced species aiding the re-establishment of soil fertility in the soil of the degraded quarry. In the first growing season- since facilitation was evident amongst *T. subterraneum* as a nurse plant and as a target plant- a suitable strategy to restore the soil could be via planting it as a pure stand of foundation species (Coiffait-Gombault et al., 2012). With its ground-hugging nature, *T. subterraneum* will spread on the soil surface, restraining ruderal weeds present in the soil seed bank (Walker et al., 2004), and reduce soil erosion (Novara et al., 2011). Ultimately, being an annual, it will set seeds, die and dry at the end of the growing season. Hence, not exercising any competition with any newly germinated target plant seedlings.

Nevertheless, more OM must be incorporated in soil for quarry restoration, rather than depending on cultivating *T. subterraneum* alone. The dried plant biomass should then be incorporated into the soil to improve various desired properties such as soil texture, structure, OM, C, N, etc. Hence, the practice of grazing and trampling by sheep or goat flocks are currently used in quarries encouraging microbial growth and activity, ultimately increasing soil fertility and quality (Luna et al., 2016). Such a grazing pattern would perform a dual purpose: 1) Trampling and hence the light incorporation of the dried biomass of *T. subterraneum* (as a source of OM) into the top 10 cm soil layer, and 2) The increase of different forms of N in the soil by the defecation and urination of the animals, allowing more soil enrichment (Semmartin et al., 2010) with an already deficient element- Nitrogen. At the beginning of the second year, the intended seed mixture for restoration could be then seeded on site. It deserves remarking that during the second growing season, the germinated *T. subterraneum* seeds would naturally decrease in the presence of perennials and annual grass that would compete with the clover for water (Dear and Cocks, 1997).

4.4. Conclusion

This study, performed under ex-situ conditions, could help formulate a better comprehension of plant-plant cooperation. Such plant interactions are not only associated with plants communities in semi-arid Mediterranean grasslands (Génin et al., 2021; Martin et al., 2022) but might also shed some light on the possible use of a native plant, from that same habitat, as a potential nurse plant to facilitate the rehabilitation of such degraded systems (Saby et al., 2024, 2025). Outcomes showed that competition, rather than facilitation, dominated the interaction amongst the studied plant species, resulting in heterogeneous responses amongst different species and various measured traits. Nevertheless, it is possible to conclude that such manipulations could yet be another significant step in the advancement of both fundamental and experimental research. Such results could also provide diverse ways and means that might aid in detecting potential nurse plant species or structuring species that are capable of increasing the successional dynamics of a plant community. Although such ex-situ studies cannot substitute in-situ experimentations, they could be the first steps in selecting different designs, management methods, and species needed to utilize in any ecological restoration procedure, with less costly in-situ settings.

However, more comparative knowledge on the in situ species-specific effects on restored plant community and soils is still required. Our study provides just evidence for the positive relationship between *T. subterraneum* dry organic matter incorporation with N, C, P_2O_5 soil

contents but also the competition ability of *T. subterraneum* against some native target plant species of Mediterranean dry grassland restoration in Lebanon.

CRediT authorship contribution statement

Houssam Shaiban: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thierry Dutoit:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Elise Buisson:** Writing – review & editing, Validation, Formal analysis, Data curation. **Tania De Almeida:** Writing – review & editing, Validation, Formal analysis, Data curation. **Carla Khater:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing 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.

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Data availability

The data that support the findings will be available in Zenodo at [<https://zenodo.org>] following a [6 month] embargo from the date of publication.

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