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ABSTRACT

Active ecological restoration of Mediterranean semi-natural grasslands faces challenges such as limited seed dispersal and poor establishment of dominant perennial species. The aim of our study was therefore to test different seedling type along a gradient of nature-based solutions including a commercial seed mixture with seeds of regional provenance, hay transfer, and seeds from ant refuse piles both harvested in neighboring non-degraded grassland. The primary objective was to compare these three mixtures ex situ, in a greenhouse, in order to distinguish the effects of each sowing treatment under controlled common conditions with the same experiment conducted in situ across four sites in the Crau Plain (Southern France). Using a set of soil rehabilitation treatments, we compare alluvial quarries backfilled with former grassland or orchard soils, abandoned orchards treated with normal or deep plowing, and the reference grassland. In the short term (6 months), results already differed significantly between in situ and ex situ experiments. Ex situ, the commercial mixture showed significantly higher density than the other treatments and a high species richness. On the other hand, in situ, sowing from hay transfer and ant refuse piles displayed higher species richness, with a composition more similar to the reference grassland, while the commercial mixture remained similar to controls. These results underline the predominant impact of habitat conditions in constrained ecosystems, highlighting the importance of increasing the use of more nature-based solutions such as hay transfer or ant refuse piles spreading to maximize grassland restoration success.

1 | Introduction

In a context of global pressures from anthropogenic climate change and biodiversity loss, where ecological restoration is an essential complement to conservation (Bullock et al. 2011), grasslands are increasingly recognized as critical assets for sustaining a biodiverse, resilient, and healthy planet (Staude et al. 2023). Grasslands are one of the main terrestrial ecosystems, covering close to one-third of the Earth's surface (Wilsey 2021). Natural and semi-natural grasslands can be biodiversity hot spots supporting both plant and animal communities (Petermann and Buzhdygan 2021). However, they are among the most endangered habitats and have undergone significant destruction or deterioration due to a variety of human-induced factors such as intensive agriculture, urbanization, industrialization, military activities, habitat fragmentation, invasive species, land abandonment, and climate change (Gang et al. 2014; Steffen et al. 2015; Tölgyesi et al. 2022; Yang et al. 2019). These pressures have led to a drastic decline of their area, plant and insect diversity, biomass, and soil quality (Li et al. 2017; Ruan

et al. 2021; Yang et al. 2019), threatening the stability of their specific communities and the functioning of these ecosystems (Bardgett et al. 2021; Wang et al. 2017).

Grassland restoration can substantially contribute to reducing extinction risk of plants, while increasing biodiversity and providing a variety of ecosystem services essential to combating climate change such as erosion prevention, fodder production, and carbon sequestration (Bengtsson et al. 2019; Diekmann et al. 2019; Klaus et al. 2016). As carbon sequestration by grasslands increases with biodiversity, restoring grasslands addresses both biodiversity and climate crisis (Seddon et al. 2021; Staude et al. 2023).

In a context of economic and energy crisis, grassland restoration efforts should prioritize nature-based solutions to align with the challenges posed by ongoing global change and biodiversity loss (Borer and Risch 2024). These solutions rely on methods, practices, or techniques that mimic natural processes making them more cost-effective and sustainable than expensive conventional alternatives based on civil engineering, which emits CO_2 and consumes non-renewable resources (Quintero-Angel, Cerón-Hernández, and Ospina-Salazar 2023). Nature-based solutions (NbS) use ecosystems and the services they provide to address socio-ecological challenges such as climate change, food security, or natural disasters. The IUCN defines NbS as: "Actions to protect, sustainably manage, and restore natural or modified ecosystems that address societal challenges effectively and adaptively, simultaneously benefiting human well-being and biodiversity" (IUCN 2016). NbS are increasingly utilized in restoration ecology due to their potential to provide cost-effective options for climate mitigation and adaptation while supporting biodiversity. However, most NbS projects currently focus on forest conservation, restoration, and afforestation (Borer and Risch 2024; Chausson et al. 2020). There is growing recognition that, in warmer, drier, and more fire-prone future conditions, grasslands may outperform forests in preserving carbon stores, while also serving as biodiversity hotspots (Borer and Risch 2024). Hay transfer has already been employed in numerous projects for restoring grasslands (Valkó, Rádai, and Deák 2022) and is recognized as a NbS. However, further investigation is still required to understand how different kinds of NbS interventions can maintain or improve grassland biodiversity and the provision of ecosystem services amidst the challenges posed by climate change, economic, and energy crises (Lyons et al. 2023).

Among grassland ecosystems, Mediterranean dry grasslands are prime candidates for conservation and ecological restoration programs (Buisson et al. 2021). These ecosystems, considered as biodiversity hot spots, have experienced not only a decrease in their area but also a decline in habitat quality and biodiversity due to 20th century shifts in land use (Saunders, Hobbs, and Margules 1991). Our study site is located in southeastern France in the dry grassland of the Crau Plain (500 km^2) (Figure S1). This ecosystem has been severely degraded over the past 50 years by intensive orchards and quarrying (Buisson and Dutoit 2006). These activities have caused measurable changes in plant communities that persist decades after the disturbances have ceased (Helm et al. 2019; Jaunatre et al. 2016, 2023).

One of the main challenges of Mediterranean dry grassland restoration is that many grassland plant species are dispersal-limited and have low probabilities of colonizing newly established habitat patches (Buisson et al. 2021; Klaus et al. 2016; Saby et al. 2024). To overcome these limitations and promote the restoration of plant diversity through NbS, seed introduction has been established as an effective method, with a preference for utilizing species that are indigenous and collected in the local or regional area of the restoration project (Kiehl, Kirmer, and Shaw 2014; Weißhuhn et al. 2012). Commercial mixtures are a commonly used source of seed for restoration. However, seeds are expensive and commercially available only for a few common native species. Additionally, the energy costs of production and transport are high. These seeds often originate from distant provenances and/or are cultivated, making them less suitable for ecosystem restoration (Basey, Fant, and Kramer 2015; Vander Mijnsbrugge, Bischoff, and Smith 2010). This study is based on the observation that ecological differences among sites, along with the characteristics of local and source populations, should guide seed sourcing strategies (Gann et al. 2019). As a consequence, local plants may have a better establishment and fitness than plants of non-local origin (Bucharova et al. 2017; Vidaller et al. 2018, 2020; Weißhuhn et al. 2012). The genetic structure of populations and the genetic consequences of plant translocation should be carefully considered in restoration (Hoffmann, Miller, and Weeks 2021; Mijangos et al. 2015; Van Rossum et al. 2022), as introducing non-local populations can compromise the success of plant re-introductions (Bucharova et al. 2017; Hufford and Mazer 2003). For our first treatment, we used a regional commercial mixture (Southern Mediterranean France and Alps) which is the most frequently used restoration treatment in our study area. Although it is labeled as local by the seed company, it does not originate directly from the experimental site.

Integrating more NbS methods can enhance the establishment success of target species (Kiehl et al. 2010). Therefore, as a second treatment we applied hay transfer from the neighboring reference protected Mediterranean grassland. It has already been shown that hay transfer applied in restoration increases the similarity of plant communities to the reference ecosystem (Durbecq et al. 2022; Kiehl and Wagner 2006). Additionally, the use of fresh hay is more cost-effective compared to employing site-specific mixture, as cultivating many wild plants is difficult and seed propagation often requires several years (Kiehl et al. 2010).

The last treatment involved seeds from ant refuse piles, as ants lose, abandon, or reject a few seeds in the refuse piles around their nests. They have a high abundance of viable seeds (Bulot, Provost, and Dutoit 2016; De Almeida et al. 2020) collected within a 30 m forage radius (Cerdan 1989). It has been already proven for Mediterranean grasslands, and especially in the Crau Plain, that ant refuse piles have positive impacts on seed composition and increase species richness and seed density (Bulot, Provost, and Dutoit 2016; De Almeida et al. 2020). However, ant refuse piles have never been used as a seeding restoration treatment. Accumulation of seeds is the major effect of refuse piles, even if the potential number of non-viable seeds should not be underestimated due to their partial consumption by ants (LS pers. Obs.). Moreover, due to their high seed concentration, harvest of refuse piles can be done manually and has a smaller

impact on the donor ecosystem compared to harvesting hay flowers with a mechanical brusher, which would require a much larger surface area to achieve the same seed concentration and is consequently more expensive for field collection.

We tested these different types of sowing along a nature-based gradient: (1) a commercial mixture with a local regional provenance (Mediterranean and Alps); (2) hay transfer harvested from neighboring reference grasslands, and (3) seeds from ant refuse piles also harvested in neighboring reference grasslands. These treatments were implemented in situ across four sites with different soil disturbances representative of the Crau Plain dry grasslands (Buisson and Dutoit 2006), and our reference ecosystem, the non-degraded dry grassland. Simultaneously, seeds from all treatments were sown ex situ in a greenhouse in trays under optimum climatic conditions of heat, photoperiod, and water requirements using the soil collected from the five experimental sites. This experiment will aimed to understand the mechanisms promoting the recruitment and establishment of seeds of target species typical of the dry grassland, while achieving the most sustainable restoration and minimizing environmental in situ local impact. Specifically, we seek to understand variations in plant community characteristics (including composition, species richness, and evenness) between ex situ and in situ conditions. Additionally, the study aims to better understand the composition of different mixtures under optimal conditions (climate, soil) in ex situ settings. It also examines these mixtures under habitat effects, excluding grazing, in situ over the short term (6 months). This comparison between ex situ and in situ conditions will help prioritize the effects of treatments (seedling composition and germination rates) over the influence of habitat conditions in the very short term (6 months).

2 | Materials and Methods

2.1 | Research Area

The Crau Plain, the only sub-steppic Mediterranean dry grassland in southern France, represents the dry grasslands of the Northwestern Mediterranean Basin (Figure S1). It features a Mediterranean climate with low annual rainfall (400–600 mm), high wind speeds, and a unique soil structure, fostering a species-rich vegetation dominated by *Brachypodium retusum* and *Thymus vulgaris* (Buisson and Dutoit 2006) (Supporting Information S1).

2.2 | Experimental Field Design—In Situ

Experimental sites were located in La Ménudelle quarry (Figure S1), including the neighboring reference ecosystem: the non-degraded grassland; and four sites with different disturbances and soil rehabilitation treatments. Two of the test sites were formerly exploited by an alluvial quarry, backfilled for soil rehabilitation with inert materials and with (1) 40 cm of the topsoil from the previously existing grassland in 2010 and (2) 40 cm of soil from previously intensive peach orchards in 2015 (Figure S2). For these two sites, the quarry exploitation took place between 2000 and 2010. The other two disturbed sites are two former intensive peach orchards where soil rehabilitation has consisted of (3) a normal plowing of 15 cm, and (4) a deep plowing of 25 cm to inverse soil layers (Figure S2). Deep plowing or soil inversion would bury the undesirable seed bank and potentially dilute some of the chemical elements present in the soil in high concentration after cultivation, such as available phosphorus or potassium (Chenot-Lescure et al. 2022). The two former orchards had been cultivated for 13 years and were removed between 2008 and 2009. All the different sites were grazed by itinerant traditional sheep management system just after the end of soil rehabilitation.

On each site, 4 treatments (3 sowing treatments + control) were randomly replicated 6 times (120 plots in total) in 5 independent block of 21 × 15 m located in the center of each site and each of them separated more than several 10 m. Seeds were sown at a density of 15 g/m^2, which was equivalent to different quantities of material to be sown depending on the treatment (Table S1). Plots measure 2 × 2 m and are spaced 1 m apart to avoid edge effects between treatments and 2 m from the limit of the blocks. An exclosure has been set up around each block immediately after soil rehabilitation (November 2022) as it has been already proven that the absence of grazing increases seedling emergence the first years after sowing in this type of ecosystem (Buisson, Corcket, and Dutoit 2015; Vidaller et al. 2019). No soil rehabilitation or enclosure installation was done in the reference neighboring grassland which has to kept its normal and usual functioning, only the 3 sowing treatments were applied in the same way for the others four rehabilitated sites.

2.3 | Seedling Sampling

These four treatments were composed of: ant refuse piles (1) of the ant *Messor barbarus* L., which was collected by hand in September 2022 from the neighboring non-degraded reference grasslands for a total of 9.1 kg after mechanical elimination (Phytosem Company, Gap, France) of organic materials (leaves, stems, etc.). The hay transfer (2) harvest was carried out by Phytosem company using a brush over an area of around 2500 m^2 over 1 day (June 06, 2022) at the peak of seed production for this ecosystem (Bourrely et al. 1983), still in the reference non-degraded grassland for a total of 7.5 kg. This sampling was carried out in an exclosure installed in 2000 (Saatkamp, Henry, and Dutoit 2018) to maximize seed harvesting, as it was not grazed. Both seedlings were dried and arranged by Phytosem with an estimate of the percentage of seeds (Table S1). The local commercial seed mixture (3) was also prepared by Phytosem as 59% of *Poaceae*, and 41% other species for a total of 16 species characteristic of the reference grassland composition in 2 kg of pure seeds with the most local origins as possible (Table S2). The forth treatment is a control (4) with different soil rehabilitation treatments but no sowing treatment.

2.4 | Soil Parameters

In March 2022, five sub-samples of soil were collected from 1 to 10 cm depth and pooled together to reach about 100 g on each of the five different sites. Chemical parameters, physical parameters, and pH were measured by standardized methods (Supporting Information S2).

2.5 | Soil Surface Vegetation

In May 2023, surveys were performed using the regional flora of (Pavon and Pires 2020) in 1 × 1 m quadrats positioned in the center of each plot to avoid edge effects with the border, estimating the percentage cover for each plant species (24 plots per site, totaling 120 plots).

2.6 | Greenhouse Experiments—Ex Situ

In January 2023, 25 L of soil samples were collected from each site, dried, and sterilized to eliminate the natural soil seed bank. These samples were placed in a greenhouse, mixed with vermiculite to prevent compaction, and filled into trays, each containing 3.312 L of the soil-vermiculate mixture. The experiment included 75 trays with five replicates per site and treatment, with seeds sown at a density of 10 g/m^2 (Table S1). Over 5 months, seedlings were regularly identified, counted, and removed to assess germination and growth under these controlled conditions (Supporting Information S3).

2.7 | Statistical Analysis

Univariate analysis were performed using Lmer function (lme4 package (Bates et al. 2015)) by including random quadrats in the model. Normality was checked using a Shapiro–Wilk test (stats package (R Core Team 2022)). If normality assumption was not verified, tests were log transformed for soil analyses and the other tests were performed using glmmTMB (glmmTMB package (Brooks et al. 2017)). All analyses were followed by a pairwise comparison test using Sidak adjustment. Post hoc tests were made using cld (multcomp package (Hothorn, Bretz, and Westfall 2008)) and emmeans functions (emmeans package (Lenth R 2022)), and estimates were found using pairs function (graphics package (R Core Team 2022)). For the ex situ experiment, univariate analyses tested sites and treatments effects on species richness, abundances, and evenness index. Interactions between sites and treatments were also tested. For in situ data, univariate analysis tested sites and treatments effects on species richness, evenness index, vegetation cover, stone cover (only for the site effect), litter cover (only for the site effect), bare ground cover, high mean vegetation, and physico-chemical parameters. Interactions were tested between sites and treatments for the species richness and evenness index. These tests were also assessed with a nested effect (between treatments within each site and between sites within each treatment).

Plant community composition was analyzed using a non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarities (vegan package (Oksanen et al. 2022)) calculated on percent cover data for in situ data and on the presence/absence of each species for ex situ data. Species displayed on the NMDS graphs are selected using the multipatt "IndVal" function (indicspecies package (Cáceres and Legendre 2009)). Differences between treatments were tested with a permutation multivariate analysis using the pairwise.adonis2 function (pairwiseAdonis package (Martinez Arbizu 2017)); stress and R^2 are also taken into account. For ex situ data, this test investigated differences between treatments and between sites. For the in situ experiment, test was run between treatments and the reference grassland community within each rehabilitated site in the first instance and secondly between sites.

All data analyses were performed using the statistics software R 4.2.4 (R Core Team 2022). Graphical representations were drawn using ggplot2 (Wickham 2016) and Renaudpack2 (Jaunatre 2023).

3 | Results

3.1 | Soil Parameters

For soil chemical parameters, the quarry with former grassland soil showed significant lower values of CEC, OM, carbon, C:N, and nitrogen. On the contrary, this site showed significant higher values of $CaCO_3$ and CaO followed by the quarry with former orchard soil. A gradient could be observed for concentrations of P_2O_5Olsen and K_2O, with lower values for the reference grassland, followed by the quarry with soil grassland, the quarry with orchard soil, the orchard with deep plowing, and then the normal plowing. Both pH had significant higher values for former quarries. The grassland and the quarry with grassland soil had the significant higher concentrations of Na_2O. Finally, carbon and nitrogen showed significant higher values for the site quarry with grassland soil (Table 1d).

3.2 | Concentrations of Seeds Per Treatment

Out of a total of 2 g of the ant refuse piles, the total mass vegetation outside of seeds was 1.62 g with 767 seeds for 0.38 g; 544 seeds were indicated as viable and 223 seeds as non-viable (Table S1). The percentage of seeds after recalculation for the ant refuse piles would therefore be around 20% (19.23%) instead of 50% announced after sorting realized by the seed company. For the commercial mixture, on 2 g of mixture, there was 1.51 g of vegetation with a total number of seeds of 505 for 0.49 g (Table S1). This represented a percentage of seeds in the mixture of around 25% (24.62%) instead of 30% announced after sorting realized by the seed company.

3.3 | Short-Term Ex Situ Plant Species Richness and Plant Community Composition

A total of 67 vascular species have been identified for all treatments and sites after 6 months of growing in the greenhouse. Species richness was significantly higher for the hay transfer (15.12 ± 0.56) than for the local commercial seed mixture (11.04 ± 0.33) and lower for the ant refuse piles (7.88 ± 0.65) (Figure 1a). Abundance of seeds was significantly higher for commercial seed mixture (308.44 ± 15.33), then for the hay transfer (86.60 ± 5.16), and then for the ant refuse piles (17.48 ± 1.63) (Figure 1b).

The NMDS on the effect of treatments on ex situ experiment was significant (stress = 0.1552; $R^2 = 0.6341$; $p < 0.001$; Figure 2) as well as between each treatment (Table S3a). The hay transfer seedling was composed of characteristic tall sub-steppic

TABLE 1 | Chi-squared values and significance levels for effects of sites and treatments on plant community: (a) vegetation ex situ; (b) vegetation in situ; (c) cover and height in situ. The effect of the treatments was calculated by taking into account all the sites and then each site individually. Similarly, the site effect was calculated for all treatments and then for each treatment individually; (d) soil chemical parameters; (e) soil physical parameters ($p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns not significant).

(a) Vegetation ex situ

	Species richness	Evenness	Abundance
Sites	7.82.	0.77 ns	1.93 ns
Treatments	56.89***	0.16 ns	882.93***
Sites × treatments	3.84 ns	0.02 ns	5.06 ns

(b) Vegetation in situ

	Species richness	Evenness
Treatment effect:		
All sites	60.36***	0.75 ns
Referent grassland	1.88 ns	2.55 ns
Quarry former grassland soil	26.48***	5.03 ns
Quarry former orchard soil	64.18***	2.07 ns
Orchard deep plowing	66.63***	14.93**
Orchard normal plowing	33.79***	5.32 ns
Site effect:		
All treatments	131.84***	14.55**
Hay transfer	30.97***	16.52**
Ant refuse piles	18.94***	3.31 ns
Commercial seed mixture	88.97***	9.18.
Control	76.14**	12.71*
Sites × treatments	27.57**	21.09*

(c) Cover and height in situ

	Vegetation cover	Bare ground cover	Stone cover	Litter cover	Mean plant height
Treatment	15.92**	20.13***	—	—	9.68*
Site	20.17***	40.56***	80.19***	22.43***	31.45***

TABLE 1 | (Continued)

(d) Soil chemical parameters										
CEC	**pH water**	**pHKCl**	**OM**	**p2o5olsen**	**P2O5**	**K2O**	**CaO**	**Na2O**	**Nitrogen**	**Carbon**	**CN**
82.613***	223.47***	376.83***	33.289***	103.08***	122.57***	69.844***	812.13***	21.977***	38.09***	33.289***	19.117***
(e) Soil physical parameters											
Total limestone		**Clay**		**Fine silt**		**Coarse silt**		**Fine sand**		**Coarse silt**	
230.83***		19.573***		7.6874 ns		30.526***		6.337 ns		16.247**	

species such as *Avena barbata*, *Thymus vulgaris*, *Aira cupaniana*, *Brachypodium retusum*, *Brachypodium distachyon,* or *Tolpis barbata*. The composition of the ant refuse piles was also characterized by typical sub-steppic species but smaller such as *Vulpia sp.*, *Galium murale*, *Galium parisiense*, *Lysimachia linum-stellatum*, and *Rostraria cristata*. For the commercial seed mixture, no germination was identified for two species: *Echium vulgare* and *Teucrium chamaedrys*. Five species had almost no germination: *Euphorbia cyparissias*, *Hyssopus officinalis*, *Lobularia maritima*, *Melica ciliata,* and *Thymus vulgaris*. Dominance (> 10%) of three species was measured for *Dactylis glomerata*, *Bromus hordeaceus,* and *Lolium rigidum*, which was not listed in the mixture species list (Figure 3). In the end, we had consistent germination proportions for only *Bromus hordeaceus* and *Lobularia maritima* (Figure 3; Table S2).

3.4 | Short-Term In Situ Plant Species Richness and Plant Community Composition

A total of 186 vascular species have been identified on the field in the beginning of May 2023 for all treatments and sites, 6 months only after sowing in the beginning of November 2022. Species richness was significantly higher in the reference grassland (33.87 ± 1.21), then in the quarry rehabilitated with former grassland soil (29.04 ± 1.52) and the former orchard with deep plowing (26.87 ± 1.46), and finally for the former quarry rehabilitated with orchard soil (22.67 ± 1.28) and the former orchard with normal plowing (21.25 ± 1.10) (Figure 4a). Overall, the same trend was observed for the effect of sites on plant species richness when treatments were considered independently of one another (Figure 5a; Table 1b). Treatments hay transfer and ant refuse piles had significantly higher species richness (respectively 32.03 ± 1.09 and 30.43 ± 1.06) than the commercial seed mixture and control (respectively 22.37 ± 1.19 and 22.13 ± 1.34) (Figure 4b; Table 1b). As with the site effect, the same trend could be observed for the effect of treatments on species richness, taking the sites separately (Figure 5b; Table 1b).

NDMS on plant communities based on treatments was always significant: (1) for the former quarry site rehabilitated with former soil grassland (stress = 0.2117; $R^2 = 0.5651$; $p > 0.001$; Figure S3a) as well as between each treatment (Table S3b); (2) for the former quarry site rehabilitated with former orchard soil (stress = 0.1850; $R^2 = 0.6616$; $p < 0.001$; Figure S3b; Table S3c); (3) the former orchard with deep plowing (stress = 0.2044; $R^2 = 0.6224$; $p < 0.001$; Figure S3c; Table S3d) and (4) the former orchard with normal plowing (stress = 0.1816; $R = 0.6051$; $p < 0.001$; Figure S3d, Table S3e). The same trend was observed for all four rehabilitated sites, the reference was characterized by typical xeric sub-steppic species. The two treatments closest to the reference grassland in terms of species composition were the ant refuse piles and the hay transfer. The ant refuse piles was composed of typical Mediterranean small dry grassland species, and the hay transfer was mostly composed of tall *Poaceae* species. The commercial seed mixture and control seemed to be the two sowing treatments furthest from the grassland in terms of species composition.

Among the species of commercial seed mixture encountered in the field, we could observe a dominance of two species in terms

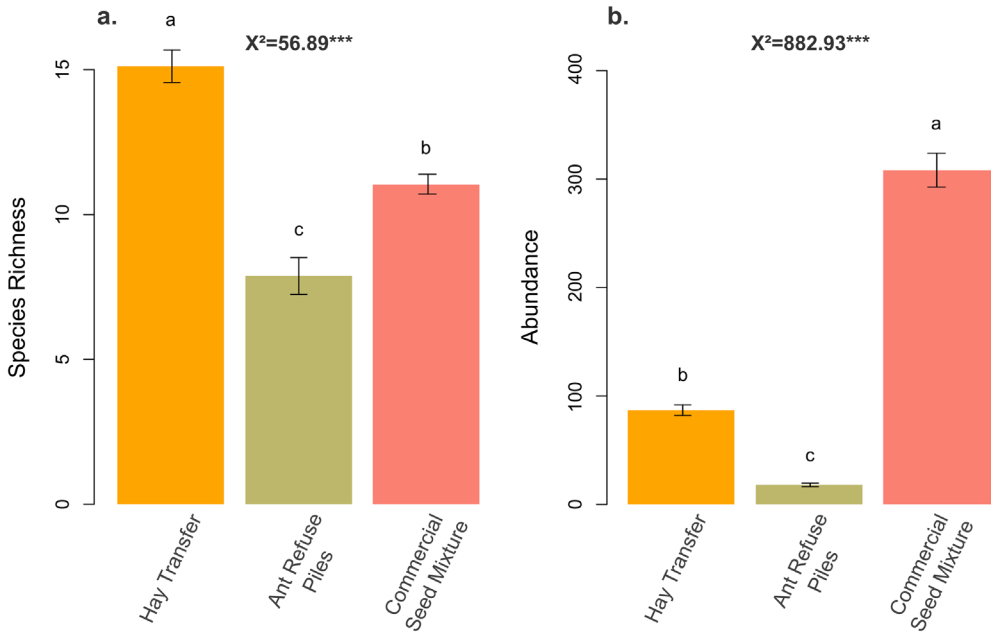

FIGURE 1 | Species richness (a) and abundances (b) according to treatments for a tray of 24 × 34.5 cm. Significant differences between average of each group are indicated with different letters, calculated with glmmTMB followed by a pairwise comparison test using Sidak adjustment. The given statistics are estimates, accompanied with stars (*** < 0.001). [Colour figure can be viewed at wileyonlinelibrary.com]

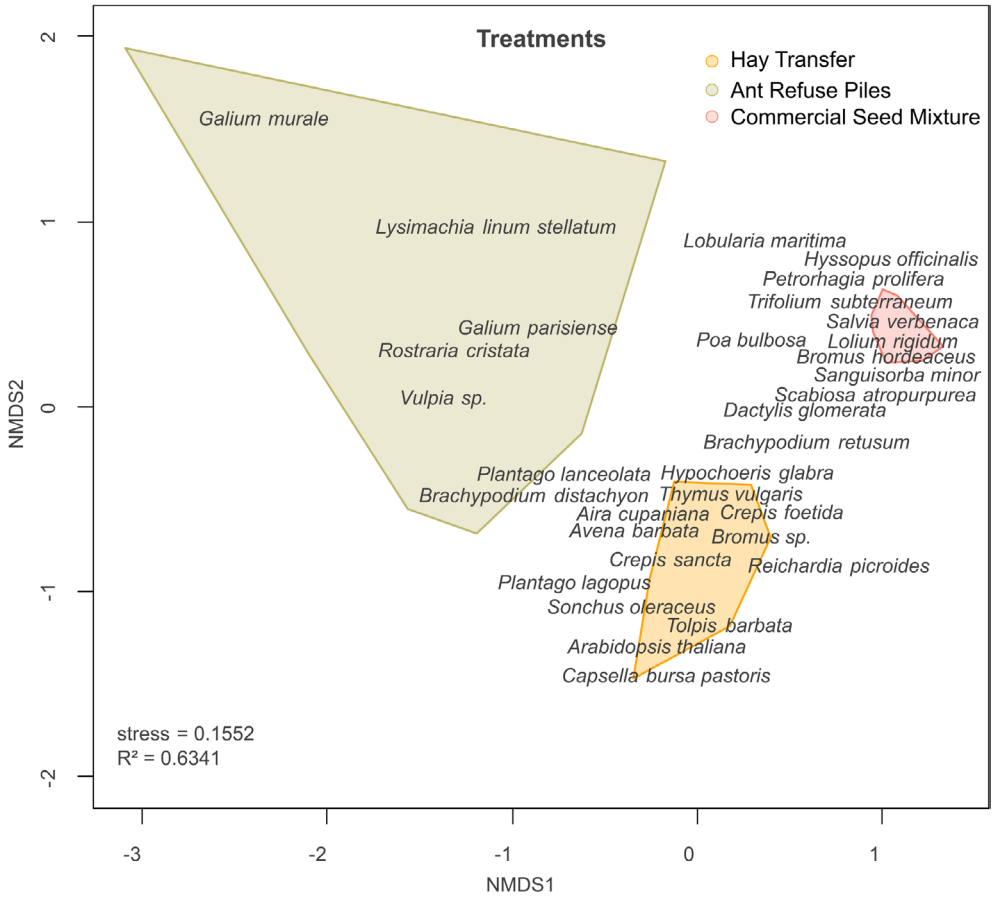

FIGURE 2 | Non-metrical multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities of ex situ plant composition for each treatment: Hay transfer, ant refuse piles, and commercial seed mixture. The polygons illustrate the projection of vegetation zones on the NMDS. [Colour figure can be viewed at wileyonlinelibrary.com]

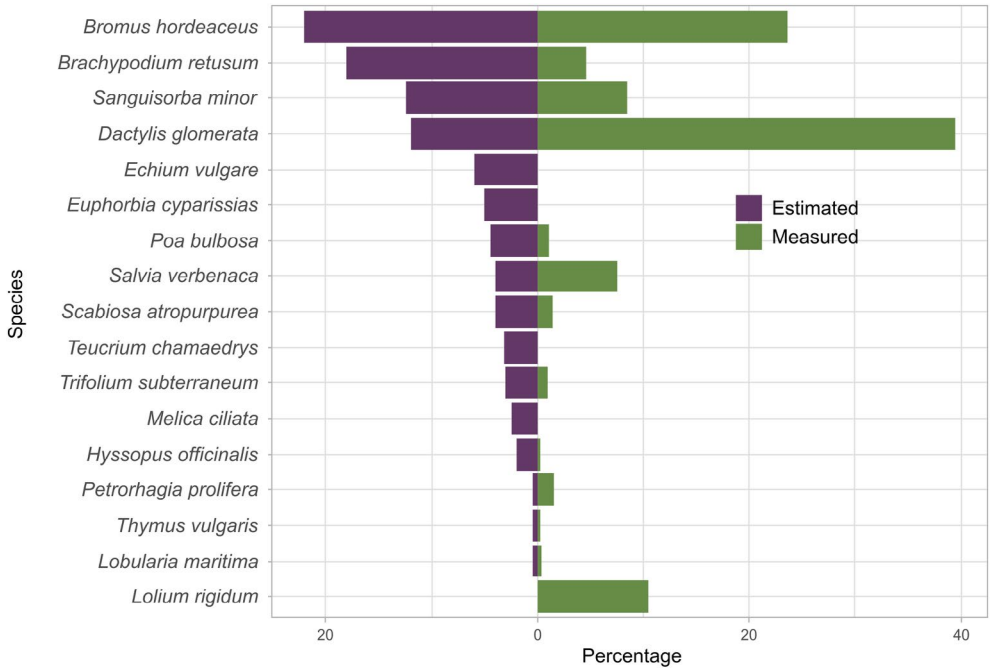

FIGURE 3 | Percentage abundance of seeds of each species advertised by the seed company on the left in purple and of ex situ germinated seedlings for all soils on the right in green. [Colour figure can be viewed at wileyonlinelibrary.com]

of cover (>10%): *Bromus hordeaceus* and *Sanguisorba minor* (Figure S4). Three species included in the species list were never found in the field, and eight species had very low cover (<2%) (Figure S4).

The NMDS carried out on the different sites is significant (stress = 0.1861; $R^2 = 0.3132$; p value < 0.001) as well as between each site (Figure 6; Table S3f). A gradient in the plant composition could be observed from the reference grassland to the former orchard with deep plowing. The site nearest the reference grassland was the former quarry rehabilitated with former grassland soil, followed by the former quarry rehabilitated with former orchard soil, the former orchard with deep plowing, and then the former orchard with normal plowing (Figure 6; Table S3f).

3.5 | Short-Term In Situ Vegetation, Bare Ground, Stone, and Litter Covers

Total vegetation cover was significantly higher for the grassland and the two former orchards, as well as for the commercial seed mixture (Figure 4; Table S3c). On the contrary, bare ground cover was lower for this treatment and for the reference grassland site (Table S3c). Stone cover was higher in the reference grassland site, followed by the two former rehabilitated quarries. Litter cover was higher in the reference grassland. The site with the highest average vegetation height was the former orchard with deep plowing, followed by the former orchard with normal plowing, and the former quarry rehabilitated with former orchard soil. Finally, the average vegetation height was higher for the hay transfer (Table S3c).

Vegetation cover during the 6 months survey among treatments followed the same trend between rehabilitated sites (Figure S5). The commercial seed mixture had the highest vegetation cover, followed by the hay transfer; the ant refuse piles and the control had close vegetation cover over time. All treatments were witnessing a drastic vegetation cover decrease between 13/04 and 17/05. This decrease was even more important for the commercial seed mixture for orchard soils, which represented the lowest vegetation cover at 17/05 for both former orchards.

4 | Discussion

Even in the short term (6 months), our results showed a strong difference between the ex situ and in situ experiment for the different restoration treatments tested.

Soil samples origin did not significantly influence species abundances or composition in the ex situ experiment, consistent with findings by Zylberberg, Rotem, and Ziv (2024). Under optimal conditions, including an unlimited water supply, the effect of soil moisture limitations typical of Mediterranean soils was eliminated (Vidaller et al. 2019), neutralizing the effects of in situ soil parameters.

For plant communities, under optimal conditions, the local commercial mixture performed well, showing the highest seedling abundance in the ex situ experiment. However, this treatment did not exhibit the greatest species richness, which was observed in the hay transfer treatment. Furthermore, the local commercial mixture was characterized by an overrepresentation of certain species (*Dactylis glomerata*, *Bromus hordeaceus*, *Lolium rigidum*) compared to the proportions listed by the seed company.

The ex situ experiment also revealed an underestimation of seed concentrations in the other two treatments: the hay transfer and

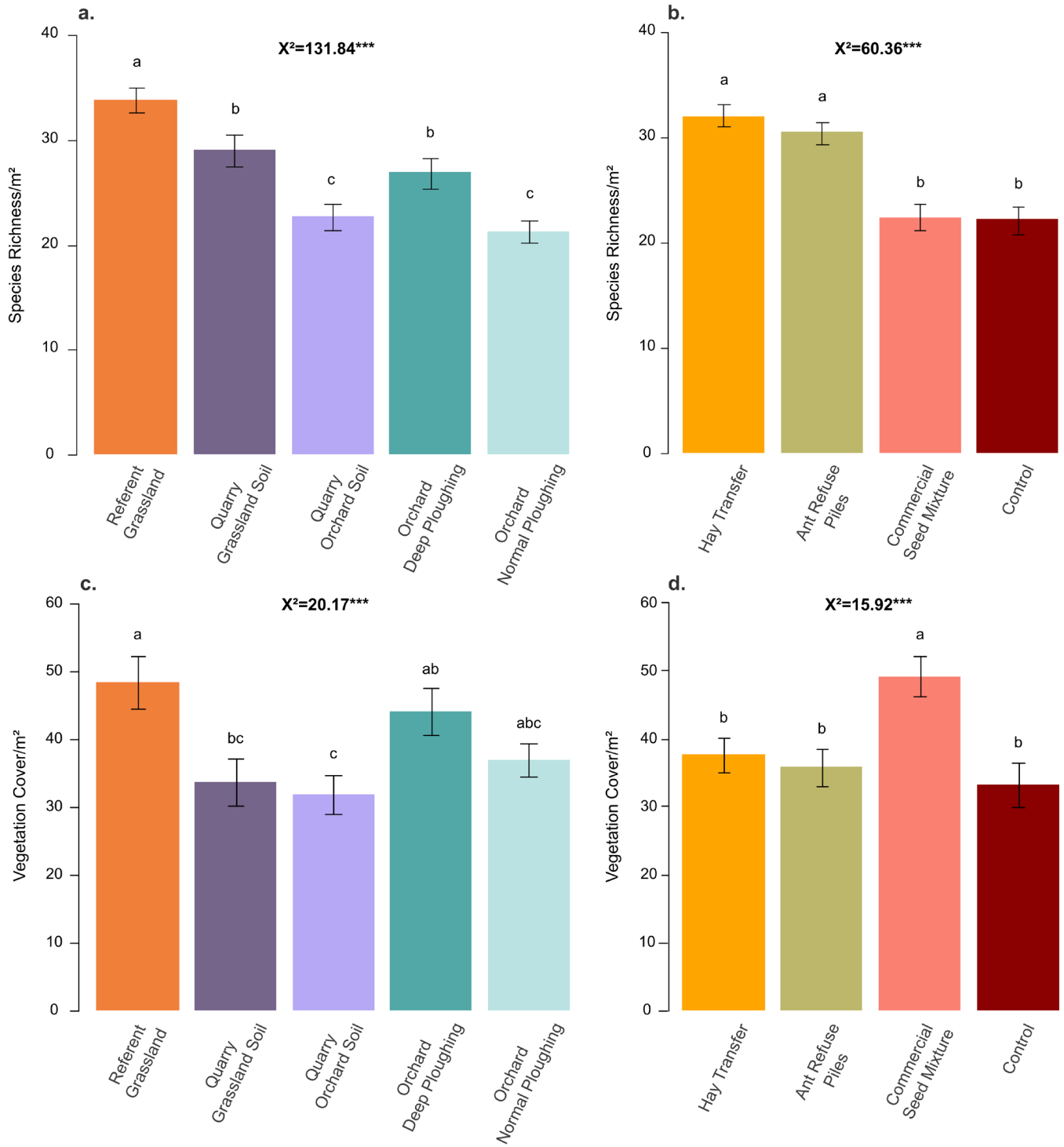

FIGURE 4 | Species richness and vegetation cover according to sites (a, c) ($N = 24$) and to treatments (b, d) ($N = 30$). The species richness given corresponds to the number of species found in $1m^2$, and the vegetation cover is an estimated percentage. Significant differences between average of each group are indicated with different letters, calculated with glmmTMB followed by a pairwise comparison test using Sidak adjustment. The given statistics are estimates, accompanied with stars (*** < 0.001). [Colour figure can be viewed at wileyonlinelibrary.com]

the ant refuse pile treatment. This was most pronounced in the ant refuse piles, where a high proportion of non-viable seeds led to low seedling abundance. Nevertheless, the ant refuse piles exhibited species of the reference grassland (Bulot, Provost, and Dutoit 2016) that were absent in the hay transfer treatment. The ant refuse piles were mostly collected in grassland micro-sites corresponding to local biological crust (Rieux, Ritschel, and Roux 1977) which are composed of very short species and are characteristic of our reference ecosystem (Martin et al. 2022).

The underestimation of the concentration of seeds in the hay transfer has consequences on the number of germinations and therefore on the abundances found in the trays compared with the commercial mixture. However, this is still the treatment

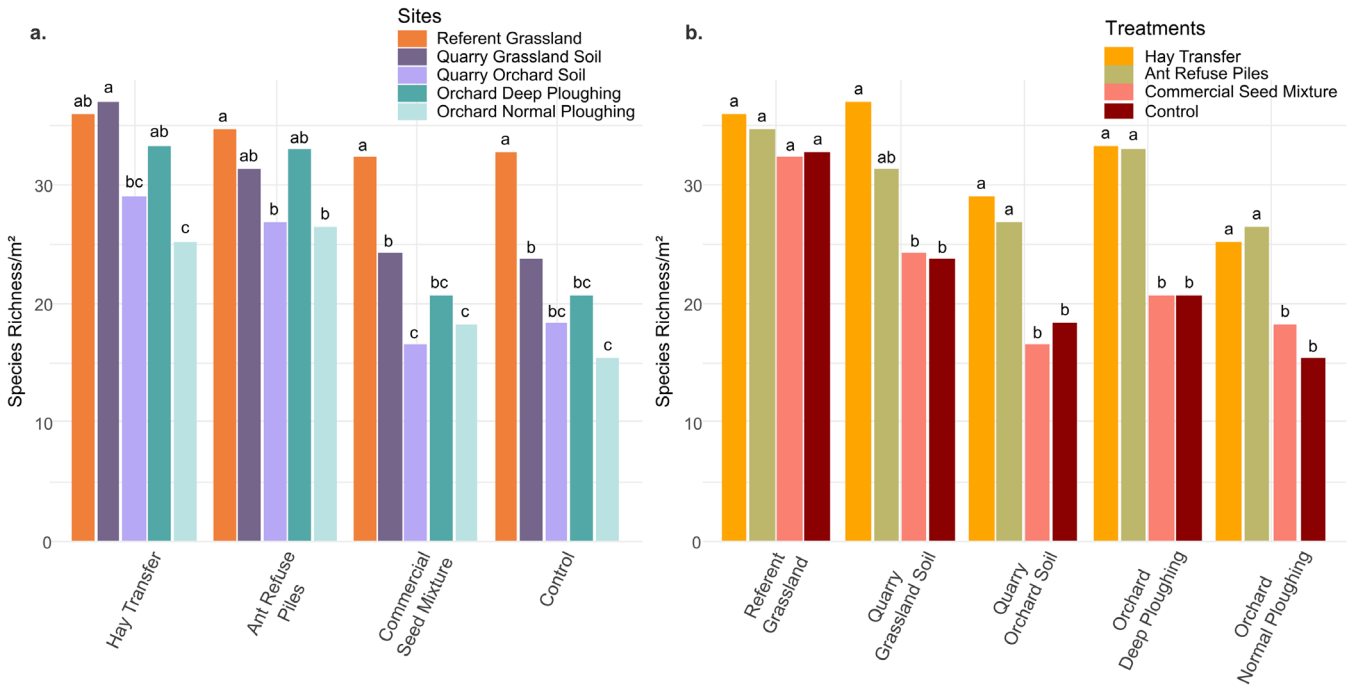

FIGURE 5 | Species richness according to sites within each treatment and species richness according to treatments within each site. The species richness given corresponds to the number of species found in $1m^2$ ($N=6$). Significant differences between average of each group are indicated with different letters, calculated with glmmTMB followed by a pairwise comparison test using Sidak adjustment. [Colour figure can be viewed at wileyonlinelibrary.com]

where the greatest number of species were found (Coiffait-Gombault, Buisson, and Dutoit 2011). Nevertheless, most of the species found were tall *Poaceae* (Jaunatre, Buisson, and Dutoit 2014), mainly due to the harvesting method (brush machine) and the fact that the harvest was carried out in an exclosure where the absence of grazing since 2001 has favored the expression of tall *Poaceae* plants (Saatkamp, Henry, and Dutoit 2018). Some species were also found in the two nature-based treatments.

For in situ experiment, in terms of soil parameters, three groups emerge from the results of soil analyses. The reference non-degraded grassland ecosystem is characterized by the typical soil of the Crau area, a Haplic Cambisol (Leptic) (Bulot et al. 2017). The former quarry with grassland soil is characterized by a more calcareous soil with a high pH due to pieces of calcareous conglomerate layer remaining in the soil after removing and replacing the topsoil. Similar results were measured during topsoil removal operations (Allison and Ausden 2004; Jaunatre, Buisson, and Dutoit 2014). These first two groups have also higher Na_2O concentrations, which can be explained by the presence of irrigation in the orchards that has entailed a dilution of this element. These results are similar to what was measured in a previous study, where Na_2O was diluted by former melon culture in this area (Saby et al. 2024). The third group, composed of the two former orchards (normal and deep plowing), is mostly characterized by fertilized soil, simply due to the fertilizing residues (phosphorus and potassium) introduced during the peach-growing period (Helm et al. 2019; Jaunatre et al. 2023; Saby et al. 2024). The former quarry with orchard soil is somewhere intermediate between the last two groups, both because it has been in contact with the calcareous matrix and is therefore also influenced by a calcareous chemistry and also because it is composed of orchard soil and therefore also has fertilize residues.

These differences between sites can also be measured for vegetation 6 months only after the application of the different treatments. The deep plowing did indeed result in a greater number and diversity of characteristic plant species of the reference grassland to emerge, probably due to a lower level of germination of undesirable spontaneous vegetation (arable weeds and ruderal species) than for the two other sites with orchard soil. The non-degraded grassland is characterized by numerous species forming a highly species-rich area (± 35 species/m^2), of the ancient and stable community (Saatkamp, Henry, and Dutoit 2021).

Concerning the different treatments, the local commercial mixture showed negative assessment under in situ conditions in the short term. We measured a less effective treatment, very close to control in terms of plant composition and species-richness. The species composition was very homogeneous, and we found the same results as for the ex situ experiment, with an over-representation of only a few species, this time dominated by *Bromus hordeaceus* and *Sanguisorba minor*. This is the treatment with the plant composition furthest from the desired composition of our reference ecosystem 6 months after sowing. In addition, a much lower species richness was measured, close to that of treatments with no seeding, mostly composed of spontaneous vegetation. As previously stated, a significant *Bromus hordeaceus* cover was noted for this treatment, which dried out as soon as it started to get warm in spring, therefore greatly reduced global vegetation cover, and led to the greatest reduction in total vegetation cover, all treatments combined. This can easily be explained by the fact that this treatment, even with the use

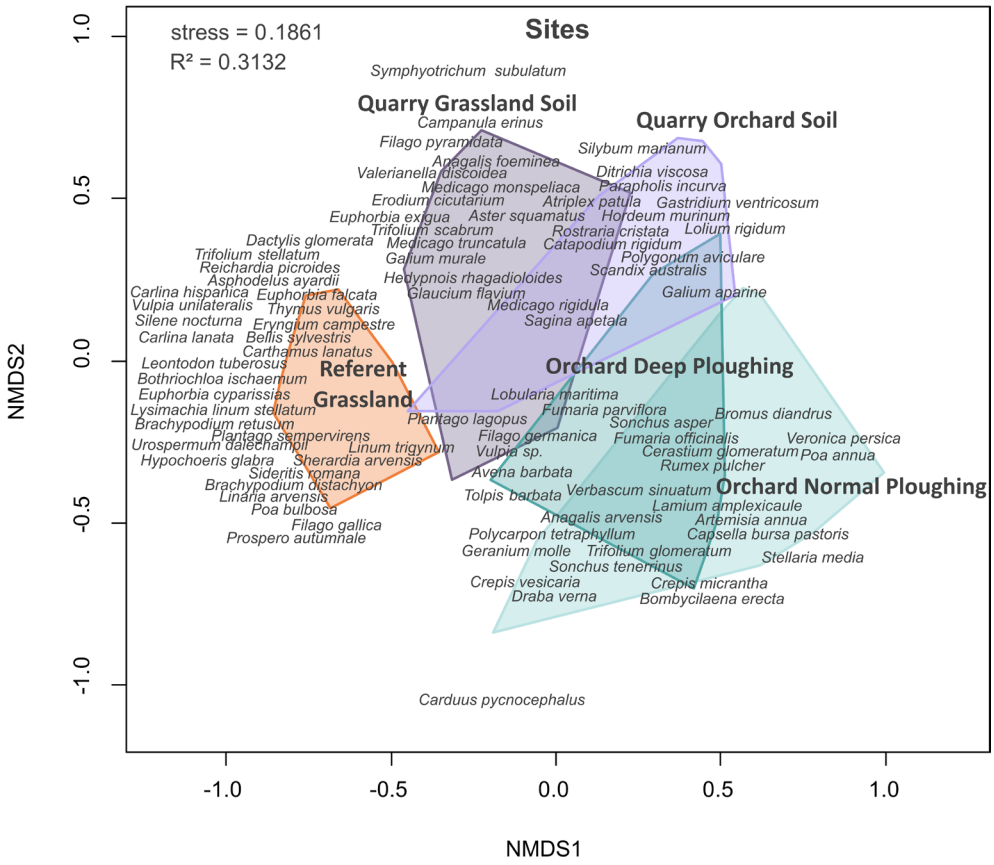

FIGURE 6 | Non-metrical multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities of in situ plant composition for each site: Former quarry with grassland soil; former quarry with orchard soil; former orchard with deep plowing; former orchard with normal plowing. [Colour figure can be viewed at wileyonlinelibrary.com]

of a local commercial seed mixture, is anyway not adapted to the local harsh environmental conditions of our ecosystem, where on the contrary local plants from the neighboring grassland perform better and are better adapted than plants of commercial origin (Oduor, Leimu, and van Kleunen 2016). This mixture may be designated as local, but its range of provenance extends across the Mediterranean basin to the Alps, ecosystems with very different abiotic conditions.

Concerning the two most nature-based treatments, despite an underestimation of the seed concentrations in the hay transfer and the ant refuse piles, species richness is much higher than the local commercial mixture and the control in the short term. Although these two treatments don't have the same species composition as already measured in the ex situ experiment (see above).

Without considering time effects in the middle term, hay transfer and the ant refuse piles are therefore promising seedlings that could be used as complementary solutions for future restoration projects involving the restoration of dry grasslands with nature-based solutions. The aim will be not to sow ant refuse piles all over the area to be restored, but to use them as nuclei, enriching the hay transfer with species such as small annual characteristics of the reference dry grassland, not found in the latter. Indeed, planting patches of vegetation (applied nucleation) is a promising approach for restoring native grassland species (Grygiel, Norland, and Biondini 2018; Holl et al. 2021). This contribution of small species typical of the Crau Plain would be a major asset to the hay transfer, which has already shown many positive results in this ecosystem (Coiffait-Gombault, Buisson, and Dutoit 2011; Jaunatre, Buisson, and Dutoit 2014). Nevertheless, further surveys are still needed to understand how the different plant communities will establish themselves and evolve over time for the in situ experiment.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.