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RESEARCH ARTICLE

Restoring stone and dominant grass species cover in a Mediterranean grassland: 20-year effects on soil, vegetation, and arthropod communities

Léa Saby^{1,2,3} , Elise Buisson¹ , Olivier Blight¹ , Christel Vidaller¹ , Thierry Dutoit¹ 

Long-term studies are needed to monitor recovery following restoration, as it may take decades or even centuries, particularly in the case of Mediterranean dry grasslands, for communities to reach their former equilibrium before the degradation occurred. A multi-component approach is also needed to evaluate restoration success and better understand the complex impacts of former restoration projects on present-day ecological interactions and ecosystem functions. The objective of this study was to address the restoration of a Mediterranean grassland in southern France, 20 years after implementation. Particularly, we examine the long-term impact on soil, vegetation, and arthropods of the reintroduction of a dominant grass species (*Brachypodium retusum*) and the restoration of the natural stone cover on a degraded former cultivated field. Soil analyses revealed that reestablishing stone cover only slightly acidified the soil, while *B. retusum* presence enhanced soil fertility. *Brachypodium retusum* also decreased the nutritional value of forage and increased plant biomass and litter. Plant composition shifted with treatments: *B. retusum* and stone cover favored xeromesophilous species, while *B. retusum* alone encouraged less palatable species. The soil seed bank composition and abundance were positively influenced by stone cover but negatively impacted by *B. retusum* reintroduction. Negative outcomes on some arthropods and mesofauna were measured in treatments with both *B. retusum* and stones, except for Acari, which were positively impacted by the presence of stones. The findings emphasize that *B. retusum* is an ecological engineer with complex effects on the different ecosystem components.

Key words: arthropods, *Brachypodium retusum*, mesofauna, plant communities, seed bank, soil, stone cover

Implications for Practice

- Evaluating Mediterranean dry grassland restoration success needs long-term and multi-component biodiversity studies.
- Reintroduction of the dominant perennial grass species (*Brachypodium retusum*) and restoration of the former stone cover did not allow the restoration of pre-existing Mediterranean dry grassland after cultivation, even in the long term (20 years).
- Understanding complex effects of ecological restoration actions on different ecosystem components (soil, flora, and arthropods) allows exploring better alternative for present-day restoration.
- *Dactylis glomerata*, a more palatable grass species than *B. retusum*, should be tested as an alternative for restoring the nutritional value and biodiversity of the pre-existing Mediterranean dry grassland.

Introduction

Grasslands are one of the dominant terrestrial ecosystems, covering close to one-third of the Earth's surface (Wilsey 2021). Natural and semi-natural grasslands are a hot spot of biodiversity, both in terms of plant and animal communities (Petermann & Buzhdygan 2021). These ecosystems have a high conservation

value (Dengler et al. 2014) and are important contributors to ecosystem services (Bengtsson et al. 2019; Diekmann et al. 2019). Grasslands have undergone significant destruction or deterioration due to various human-induced factors, such as agriculture, urbanization, invasive species, changes in management intensity, and climate change (Steffen et al. 2015; Yang et al. 2019; Tölgyesi et al. 2022). This deterioration is characterized by a decrease in plant and insect diversity, biomass, and soil composition (Li et al. 2017; Yang et al. 2019; Ruan et al. 2021)

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threatening community stability and ecosystem functioning (Wang et al. 2017; Bardgett et al. 2021).

Many restoration efforts begin by attempting to improve the degraded abiotic state in the hope that the appropriate species and ecological processes will then reestablish (Palmer et al. 1997). However, these changes may not be sufficient to restore ecosystem functions that involve both biotic and abiotic interactions (Palmer et al. 1997; Suding et al. 2004). Thus, it may be beneficial and cost-effective to introduce species that can modify the environment and have positive impacts on other species, and ecological processes to achieve conservation objectives (Byers et al. 2006). In dry grasslands, perennial grass species could improve habitats by capturing soil particles, nutrients, and microorganisms, thus facilitating the reestablishment of other species (Whisenant et al. 1995). Species can cooperate by exchanging different minerals, such as carbon, nitrogen, phosphorus, water, and even defense compounds. The process of facilitation plays a significant role in shaping interactions and connections between plants (Bertness & Shumway 1993; Bertness & Hacker 1994). Facilitative interactions are important plant regulators in their environment and community arrangement in stable environments (Gómez-Aparicio 2009; Soliveres & Maestre 2014).

Our study focuses on the sub-steppic Mediterranean grasslands of the La Crau plain, South-Eastern France (Fig. 1), representative of the 26,000 km² of dry grasslands of the Northwestern Mediterranean Basin (Buisson et al. 2021). Analyses of the impact of former crops on the reference ecosystem have already been carried out through the study of vegetation (Buisson et al. 2006; Vidaller et al. 2019; Jaunatre et al. 2023) and beetles (Fadda et al. 2004). These studies highlight that urgent conservation is needed for remaining grassland areas and that restoration efforts face significant challenges and timeframes, emphasizing the importance of understanding effective restoration strategies. Degraded plant communities have low plant species richness and a lack of natural recolonization even decades after cultivation abandonment (Jaunatre et al. 2016, 2023; Helm et al. 2019). The irreversibility thresholds crossed by the ecosystem after cultivation are the reduction of stone cover on the soil surface and the available soil phosphorus concentrations that are always significantly higher in former cultivated areas than in the reference grassland ecosystem even decades after abandonment (Römermann et al. 2005; Jaunatre et al. 2016, 2023).

Habitat quality in the Crau plain is defined by the presence of dominant perennial plants that structure the dry grassland plant community, and provide arthropods with essential resources and conditions. The quality of the habitat can be improved by restoring stone cover, which contributes to habitat heterogeneity (Brose 2003). Stones create micro-habitats on the soil surface, offering favorable soil moisture and temperature conditions, important for arthropod activity (Tauber et al. 1998). This habitat, influenced by the characteristics of the stones, favors arthropod diversity (Blight et al. 2011) and supports the growth of perennial plants, essential in dry grasslands, by enabling better root growth and protecting them from sheep grazing (Bourrelly et al. 1983). Considering these multiple interactions between habitat conditions and biodiversity, a multi-component

approach of ecosystem restoration projects is therefore essential. Until now, many studies have only investigated the effects of restoration on vegetation, but more rarely on invertebrates, which remain one of the most-under-sampled and least studied groups of terrestrial ecosystems in restoration (Wijas & Atkinson 2021; Buisson et al. 2024). It is thus important to consider multiple groups of organisms across various trophic levels (Ruiz-Jaen & Mitchell Aide 2005).

At the beginning of the 2000s, it was projected that successful restoration of the plant community structure of this degraded grassland in the Crau Plain could depend on the reestablishment of the native and dominant perennial rhizomatous grass (*Brachypodium retusum* L.). Plant vegetation cover in the reference ecosystem is composed of about 50% of this plant, which has a potential structuring role and improves habitats for other species under traditional grazing conditions (Buisson & Dutoit 2004; Coiffait-Gombault et al. 2012). *Brachypodium retusum* was sown in 2003 in an abandoned field formerly cultivated between 1972 and 1978 after having manipulated the microenvironment by restoring the natural large stone cover on the soil surface in 2001. Indeed, stones, initially present in the reference grassland, had been removed and set aside to allow cultivation of the land in the 1970s. They have been put back in place from the stone piles created in the border of the former cultivated field for the restoration of the microenvironment in the 2000s.

Ecological restoration can take decades or even centuries because community assembly and interactions need time to occur. There is usually a time lag between the work implemented in restoration projects and the time when the target ecosystem has achieved its restoration objectives. Then, long-term surveys are needed to monitor the development of the basic components and functions of the ecosystem and therefore gain perspective on the restoration work (Tischew et al. 2010).

The aim of this study is to assess the importance of reestablishing the ecosystem dominant plant species and restoring the stone cover of this Mediterranean grassland. The effects were measured over a long term (20 years), essential for measuring the effects of restoration on old dry grasslands, while including a multi-component approach to give a global view of the different treatments over time and at different trophic levels (plants, arthropods, and mesofauna). Twenty years after the experiment was set up, we revisited it to evaluate the effects of these treatments on: (i) the physico-chemical composition of the soil, plant litter, and forage; (ii) plant communities by sampling the vegetation and the soil seed bank; and (iii) soil mesofauna and ground-dwelling arthropods.

Methods

Study Area

The dry plain of La Crau (600 km²) in southern France (Fig. 1) is in the former delta of the Durance river in southern France and is currently composed of a landscape of dry grasslands, which have been used as rangelands for millennia (Buisson & Dutoit 2006). This region is characterized by a Mediterranean climate with high interannual variability, relatively low rainfall

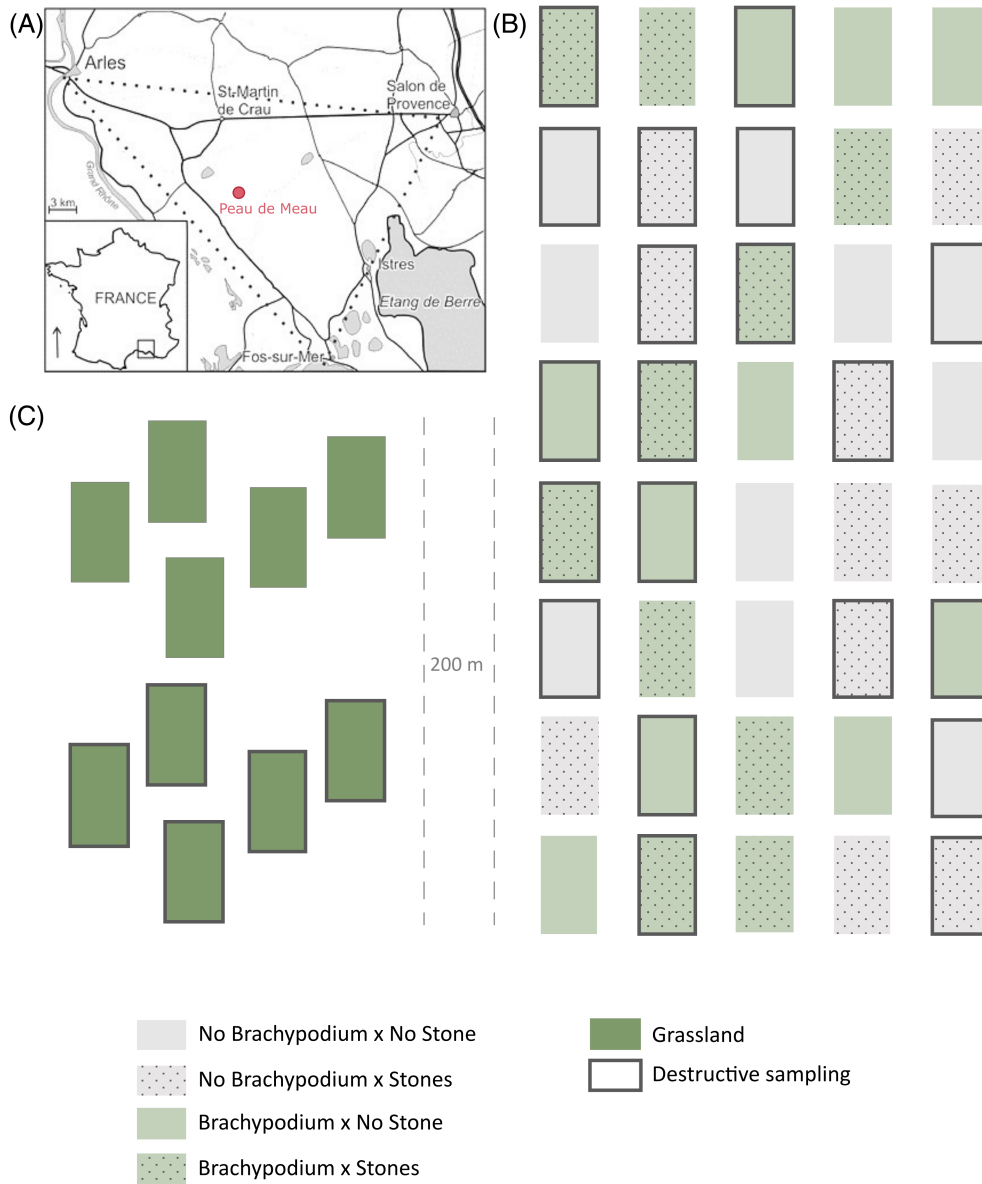


Figure 1. Geographical location of the study area and experimental design layout. (A) Map of France showing the geographical location of the study area. The dry grasslands of La Crau are inside the dotted triangle (Blight et al. 2011). (B) Experimental design layout. Five plots per treatment were randomly selected to carry out destructive sampling (soil, seed bank, litter, forage, and mesofauna) and five to carry out nondestructive sampling (vegetation survey and ground-dwelling arthropod sampling). (C) Ten plots were also randomly selected on the reference steppe: five for destructive sampling and five for nondestructive sampling.

(400–500 mm per year on average), with maxima in spring and autumn, as well as long and dry summers and mild winters (average annual temperature: 14°C). On average, the sun shines 3000 hours per year and a very strong prevailing wind, the mistral, blows from the northwest 334 days per year, which increases soil and vegetation evapotranspiration (Devaux et al. 1983). The bedrock of La Crau plain is a layer of conglomerate from 1 to 5 m thick, located 40 cm deep, which plant roots cannot penetrate (Devaux et al. 1983). It is formed by stones embedded in a limestone matrix (conglomerate). Around 50% of the soil surface is covered with stones transported by the Durance river between 2 million and 70,000 years ago

(Molliex et al. 2013). Stones create microclimates that protect the soil from great temperature variations (Bourrelly et al. 1983). These conditions have led to a vegetation dominated by perennial stress-tolerant species, such as *Brachypodium retusum*, Poaceae and *Thymus vulgaris* L., Lamiaceae, which account for 50% of the biomass, and is composed of a wide diversity of annual species (Buisson & Dutoit 2006). Itinerant sheep grazing has occurred since 2000 BP at least (Badan et al. 1995). In the 1950s, direct groundwater pumping allowed the development of early season melon agricultural production, later replaced by fruit orchards in the 1990s. These activities contributed to the fragmentation of the once homogeneous

grassland landscape, where grassland remnants are now islands in a matrix of cultivated areas (Buisson & Dutoit 2006).

Study Sites

Our study was carried out in the area of Peau de Meau (200 ha), located at the west of the plain. Two sites were selected. The first site, where the experiment was carried out, is an abandoned field (8 ha), first cultivated in 1971 with melon, then cultivated with wheat and alfalfa between 1972 and 1978, then abandoned for cultivation and put back under traditional sheep grazing. The vegetation of this site is now characteristic of abandoned xerothermic field vegetation composed of species, such as *Calamintha nepeta*, *Diploaxis tenuifolia*, *Lobularia maritima*, etc. (Römermann et al. 2005; Helm et al. 2019; Jaunatre et al. 2023). The second site is the reference grassland, which was used as a control. It corresponds to a patch (35 ha) of the semi-natural dry grassland, representative of the remaining 10,500 ha of dry grassland vegetation with its original stone cover of 50% and also currently characterized by the two dominant plants: *B. retusum* and *T. vulgaris*. Both sites were grazed by traditional roving sheep livestock (Buisson & Dutoit 2004) from March to May between 2000 and 2021.

Experimental Design

Because relationships between vegetation, arthropods, and the presence of *B. retusum* and stones have already been shown (Blight et al. 2011), 40 plots were installed on the abandoned field in 2001. Plots of 1.5 m × 3 m were set up 1.5 m minimum away from each other to limit vegetation edge effects and assigned to one of four treatments in a full factorial design (Fig. 1). We thus had 10 replicate plots for each treatment. Treatments were: Brachypodium × Stones; Brachypodium × No Stone; No Brachypodium × Stones; No Brachypodium × No Stone. For treatments with stones, stones from the 1970s, initially removed for soil cultivation, were used in treatments to recreate the original 50% grassland cover on the abandoned field. For treatments with *B. retusum*, seeds were sown. These seeds were hand collected in recently burnt areas in the neighboring hills around Aix en Provence and Marseille because we were not authorized to collect them in the protected area itself and because it was well known that *B. retusum* produces more seeds after burning (Vidaller et al. 2019).

The quantity of seeds sown on the quadrats was not the same on the quadrats with or without stones. It was assumed that stones taking up space on the ground would have artificially increased the seed density on the quadrats with stones. Therefore, the density of seeds sown was 6.5 g/m² for plots with stones and 12.9 g/m² for plots without stone. This density is slightly higher than what is usually sown, but which is justifiable given the extreme conditions of this ecosystem (Kiehl et al. 2010).

In October 2020, we randomly selected five plots among the 10 replicates per treatment to carry out destructive sampling (destructive-sampling plots: soil, seed bank, litter, forage, and mesofauna) and five to carry out vegetation survey and ground-dwelling arthropod sampling (nondestructive-sampling plots). Five pairs of

unmanipulated plots were also randomly selected on the grassland as a reference (five for destructive sampling and their five parallel for nondestructive sampling).

Soil Parameters

In October 2020, circa 20 years after the experiment was set up (including *B. retusum* sowing), three subsamples of soil were collected from the first centimeters of soil (1–10 cm depth) and pooled together to reach about 100 g on each of the 25 destructive-sampling plots (20 plots on the abandoned field and 5 plots on the reference grassland). Ten chemistry parameters (CaO, K₂O, MgO, Na₂O, CEC, P₂O₅, nitrogen, C:N, C, organic matter) and pH were measured (Supplement S1: soil parameters).

Biomass, Forage, and Litter

In October 2020, the litter was collected in one 40 cm × 40 cm quadrat randomly placed in each of the plots where destructive sampling occurred and lignin and nitrogen contents were measured, 20 plots on the abandoned field and 5 plots on the reference grassland (Supplement S2: biomass, forage, and litter).

In May 2021, forage (green biomass) was harvested from each of the destructive-sampling plots. Vegetation samples were collected, at 3 cm from the soil surface, in one 40 cm × 40 cm quadrats randomly (but not where the litter was sampled previously) placed in each of the plots where the destructive sampling was conducted (20 plots on the abandoned field and 5 plots on the reference grassland). Seven fodder parameters were analyzed (cellulose and protein content, organic matter, P, Ca, Mg, and K) and nine were calculated (UEM—forage intake, dMO—digestibility of organic matter, dcDM—cellulase digestibility of dry matter, dcOM—cellulase digestibility of organic matter, dMOde—digestibility of organic matter dMO from enzymatic digestibility, UFV—meat fodder unit, PDIE—digestible protein in the intestine limited by ration energy, PDIN—digestible protein in the intestine limited by the nitrogen in the ratio, PDIA—digestible protein in the intestine from the diet and not degraded in the rumen) (Supplement S2: biomass, forage, and litter).

Soil Surface Vegetation

In April 2021, vegetation surveys were carried out when the maximum number of vascular plant species was identifiable for 2021 spring climate conditions. Surveys were conducted in one 1 m × 1 m quadrat on each nondestructive-sampling plot by estimating the percentage cover of each species according to the six abundance-dominance classes defined by Braun-Blanquet (+, 1, 2, 3, 4, 5; Braun-Blanquet 1932) (20 plots on the abandoned field and 5 plots on the reference grassland). In each quadrat, the percentage of stone cover, vegetation, and bare ground was also estimated.

Soil Seed Bank

In January 2021, sampling of the soil seed bank was conducted. This period was chosen to sample only the semi-persistent and persistent components of the soil seed bank (seeds viable for more than 1 year in the soil) (Thompson et al. 1997).

It was sampled prior to fresh seed input in spring–summer and after most seeds have germinated under the Mediterranean climate, that is, in the fall and winter. Eight samples of 5 cm × 5 cm by 5 cm depth (total of 125 mL) were collected in each destructive-sampling plot (20 plots on the abandoned field and 5 plots on the reference grassland). The total volume per plot was 1 L, the average volume recommended (Bakker et al. 1996). Soil seed bank samples were germinated using the standard procedure (Heerd et al. 1996) (Supplement S3: soil seed bank).

Soil Mesofauna and Arthropods

Mesofauna sampling was carried out in April 2021 on destructive-sampling plots (20 plots on the abandoned field and 5 plots on the reference grassland) in one quadrat per plot (10 cm × 10 cm and 5 cm deep). They were extracted using Berlese funnels and conserved in 70% alcohol. Acari were divided into two suborders reflecting their trophic level: Oribatida (detritivores) and Gamasida (predators). Dry soil samples were weighed and the number of Acari individuals was reported to 100 g. Data were then rounded for statistical analysis. Because only eight individuals were captured, no statistical tests were carried out on Collembola.

In Mai 2021, one pitfall trap was placed at the center of each nondestructive-sampling plot for 3 weeks. The traps were 5.5 cm in diameter and 7 cm deep. They were buried up to the edge and filled with one-quarter propylene glycol. Collected individuals were identified to the order, and then to the species for Spiders, Coleoptera, and Isopods. Among the captured Collembola, only epigeous were retained in the statistical analyses.

Statistical Analyses

All data analyses were performed using the statistics software R 4.0.4 (R Core Team, 2020) and the packages *ade4*, *vegan*, *glmmTMB*, *car*, *emmeans*, *multcomp*, and *Renaudpack2*. When the response variables were analyzed using univariate models, we included *B. retusum* and stone cover as explanatory variables (presence/absence of *B. retusum* and presence/absence of stones: No Brachypodium × No Stone; No Brachypodium × Stones; Brachypodium × No Stone; Brachypodium × Stones). No interaction effects were significant; treatments were tested with an additive effect. All analyses were followed by the appropriate pairwise comparison test (Tukey or a Sidak adjustment).

Differences in levels of soil, litter, and forage variables according to the type of treatment were assessed using two-way analysis of variances (ANOVAs). For litter and plant biomass, these tests were performed with and without stone weighting. The percentage of stones was estimated and then deducted from the two masses measured (biomass and litter mass). Normality was checked using the Shapiro–Wilk test and equality of variances using Fisher and Bartlett tests. When ANOVAs were not feasible (non-normality, non-equality of variances), general linear model (GLM) were performed with a gamma error distribution.

A principal component analysis (PCA) was performed: on soil parameters (C, N, P₂O₅, K₂O, Na₂O, MgO, and pHWater), on litter mass and on forage parameters (cellulose, biomass, protein, digestibility, K, and P) depending on the treatments and grassland (control). A table of correlations was built and parameters selected to avoid redundancy.

GLM fitted with a gamma error distribution were performed to test differences in vegetation cover, stone cover, and bare ground cover depending on treatments. In order to describe the vegetation, a GLM fitted with a Poisson error distribution was performed on the species richness for the same treatments. Plant community composition was analyzed using a nonmetric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarities calculated on percent cover data to investigate differences between treatments and with the grassland (control). The analysis was carried out after removing *B. retusum* in order to identify its effects on plant composition, and after removing the species present only once for all quadrats. A total of 20 species was removed including *B. retusum*. The final matrix was composed of 25 quadrats × 46 species. Differences between treatments were tested with a permutation multivariate analysis using the Adonis function.

To describe the semi-persistent and persistent components of the soil seed bank, a GLM fitted with a Poisson error distribution was performed on species richness. To account for over-dispersion, a GLM fitted with a Quasi-Poisson error distribution was performed on abundance: the number of seedlings per treatment. A NMDS analysis based on Bray–Curtis dissimilarities calculated on number of individuals was performed to investigate differences in seed bank composition between treatments and with the grassland (control). The analysis was carried out with all the species, and the final matrix was composed of 25 quadrats × 47 species. Differences between treatments were tested with a permutation multivariate analysis using the Adonis function.

To analyze the response of soil mesofauna and arthropods to the four treatments, GLM fitted with a Poisson error distribution was performed on abundances (total Acari, Gamasida, and Oribatida; epigeous Collembola, total spiders, and spider abundances for species with more than 10 individuals; total Coleoptera and the two most abundant species; total number of Isopods and the most abundant species). GLM fitted with a Quasi-Poisson error distribution was performed when over-dispersion was observed.

Results

Soil, Litter, and Forage Characteristics

Concerning the stone cover treatment, only pH (pHKCl and pHWater) is significantly lower in the presence of stones. Plots with *Brachypodium retusum* show significantly higher concentrations in the soil of P₂O₅, K₂O, MgO, organic matter, total nitrogen, carbon, C/N, and mass litter (Table 1A & 1B). Litter mass and plant biomass without the weighting of the surface covered by stones are significantly higher with the presence of *B. retusum* and with the presence of stones (Table 1C & 1D; Fig. 2). The presence of *B. retusum* shows

Table 1. Significance levels for effects of *Brachypodium retusum* and stones according to the different treatments. (A) Cation exchange capacity (CEC); sodium oxide (Na₂O); pHKCl; pHWater; available phosphorus (P₂O₅Olsen); potassium oxide (K₂O). (B) Magnesium oxide (MgO); calcium oxide (CaO); organic matter (OM); nitrogen; organic carbon (C); carbon to nitrogen ratio (C:N). (C) Litter dry weight with and without stone cover weighting; direct lignin; total nitrogenous matter; nitrogen content according to the Kjeldhal method. (D) Biomass dry weight with and without stone cover weighting; cellulose and protein content. (E) Organic matter (OM); contents in phosphorus (P); calcium (Ca); magnesium (Mg); potassium (K). (F) Forage intake (UEM); meat fodder unit (UFV); digestible protein in the intestine limited by ration energy (PDIE); digestible protein in the intestine limited by the nitrogen in the ration (PDIN); digestible protein in the intestine from the diet and not degraded in the rumen (PDIA). (G) Digestibility of organic matter (dMO); cellulase digestibility of dry matter (dcDM); cellulase digestibility of organic matter (dcOM); digestibility of organic matter dMO from enzymatic digestibility (dMOdE). (H) Plant community species richness; seed bank species richness; seed bank abundance. (I) Stone cover; vegetation cover; bare ground cover. (J) Mesofauna: Gamasida, Oribatida, Acari, Collembola. (K) Araneae: Total Adults; *Nomisa exornata*; *Zodarion elegans*; *Titanoeca monticola*; *Mecopisthes crassirostris*. (L) Coleoptera: Total adults; *Poecilium sericeus*; *Asida sericea*. (M) Isopoda: Total adults; *Amadilidium arcangelii*. The given statistics are estimates (± SE), accompanied or not with stars (*<0.5; **<0.01; ***<0.001). Estimates less than 0.01 were rounded at 0.01. Tests were only run on abandoned field data.

| (A) Soil | | | | | | |
|------------------------|---------------------------------------|--|-------------------------|-------------------------|-------------------------------------|-------------------------|
| | CEC | Na ₂ O | pHKCl | pHWater | P ₂ O ₅ Olsen | K ₂ O |
| Brachypodium | 0.01 ± 0.01 | -3.00 ± 1.79 | 0.01 ± 0.01 | -0.06 ± 0.05 | 12.30 ± 2.90*** | 60.20 ± 14.05*** |
| Stones | 0.01 ± 0.01 | 0.40 ± 1.79 | -0.01 ± 0.01** | -0.12 ± 0.05* | -5.10 ± 2.9 | -22.00 ± 14.05 |
| Model | Gamma GLM | ANOVA | Gamma GLM | ANOVA | ANOVA | ANOVA |
| (B) Soil | | | | | | |
| | MgO | CaO | OM | N | C | C:N |
| Brachypodium | 24.50 ± 10.25* | 81.70 ± 70.79 | 0.56 ± 0.17** | 212.50 ± 85.05* | 3.26 ± 0.98** | 0.72 ± 0.26* |
| Stones | 7.10 ± 10.25 | 67.10 ± 70.79 | 0.27 ± 0.17 | 89.90 ± 85.05 | 1.57 ± 0.98 | 0.33 ± 0.26 |
| Model | ANOVA | ANOVA | ANOVA | ANOVA | ANOVA | ANOVA |
| (C) Litter | | | | | | |
| | Dry weight with stone cover weighting | Dry weight without stone cover weighting | Direct lignin | Total N | Total Kjeldahl N | |
| Brachypodium | 0.10 ± 0.02*** | | 0.02 ± 0.01** | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.03 ± 0.06 |
| Stones | 0.02 ± 0.01 | | 0.04 ± 0.01*** | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.12 ± 0.06 |
| GLM model | Gamma | | Gamma | Gamma | Gamma | Gamma |
| (D) Forage | | | | | | |
| | Dry weight with stone cover weighting | Dry weight without stone cover weighting | Cellulose | Protein | | |
| Brachypodium | 0.15 ± 0.03*** | | 0.02 ± 0.01*** | 0.01 ± 0.01*** | -0.01 ± 0.01*** | |
| Stones | 0.01 ± 0.01 | | 0.02 ± 0.01*** | 0.01 ± 0.01 | 0.01 ± 0.01*** | |
| GLM model | Gamma | | Gamma | Gamma | Gamma | |
| (E) Forage | | | | | | |
| | OM | K | P | Mg | Ca | |
| Brachypodium | -1.91 ± 0.82* | -0.07 ± 0.01*** | -1.25 ± 0.16*** | -1.05 ± 0.10*** | -2.03 ± 0.58** | |
| Stones | 1.52 ± 0.82 | 0.01 ± 0.01* | 0.44 ± 0.16* | 0.16 ± 0.10 | 0.90 ± 0.58 | |
| Model | ANOVA | Gamma GLM | ANOVA | ANOVA | ANOVA | |
| (F) Nutritional values | | | | | | |
| | UEM | UFV | PDIE | PDIN | PDIA | |
| Brachypodium | 0.10 ± 0.01*** | -0.62 ± 0.08*** | -0.01 ± 0.01*** | -0.01 ± 0.01*** | -0.02 ± 0.01*** | |
| Stones | -0.01 ± 0.01 | 0.11 ± 0.08 | 0.01 ± 0.01** | 0.01 ± 0.01*** | 0.01 ± 0.01*** | |
| Model | Gamma GLM | Gamma GLM | Gamma GLM | Gamma GLM | Gamma GLM | |
| (G) Digestibility | | | | | | |
| | dMO | dcDM | dcOM | dMOdE | | |
| Brachypodium | -0.01 ± 0.01*** | -22.02 ± 1.96*** | -22.87 ± 2.05*** | -13.77 ± 1.23*** | | |
| Stones | 0.01 ± 0.01 | 2.12 ± 1.96 | 2.53 ± 2.05 | 1.31 ± 1.23 | | |
| Model | Gamma GLM | ANOVA | ANOVA | ANOVA | | |

Table 1. Continued

| (H) Vegetation | | Seed bank | | | | |
|----------------------|-------------------------------------|------------------|------------------|-------------------|--------------|------------------|
| | Plant community Species richness | Species richness | Abundance | | | |
| Brachypodium | 0.03 ± 0.11 | 0.03 ± 0.11 | -0.32 ± 0.15* | | | |
| Stones | -0.12 ± 0.11 | -0.12 ± 0.11 | 0.48 ± 0.15*** | | | |
| GLM model | Poisson | Poisson | Quasi-Poisson | | | |
| (I) Mesological data | | Stone cover | Vegetation cover | Bare ground cover | | |
| Brachypodium | -0.01 ± 0.01* | 0.01 ± 0.01** | -0.08 ± 0.03** | | | |
| Stones | 0.01 ± 0.01*** | 0.01 ± 0.01 | -0.04 ± 0.02 | | | |
| GLM model | Gamma | Gamma | Gamma | | | |
| (J) Mesofauna | | Gamasida | Oribatida | Acari | Collembola | |
| Brachypodium | 0.01 ± 0.01 | 0.24 ± 0.29 | 0.18 ± 0.27 | -0.83 ± 0.21*** | | |
| Stones | 0.01 ± 0.01* | 0.54 ± 0.29* | 0.59 ± 0.27* | 0.03 ± 0.21 | | |
| GLM model | Poisson | Quasi-Poisson | Quasi-Poisson | Quasi-Poisson | | |
| (K) Araneae | | Total adults | N. exornata | Z. elegans | T. monticola | M. crassirostris |
| Brachypodium | -0.67 ± 0.20*** | -0.82 ± 0.27** | -1.28 ± 0.86 | -0.61 ± 0.51 | 0.56 ± 0.63 | |
| Stones | -0.23 ± 0.20 | -0.27 ± 0.26 | 0.43 ± 0.84 | 0.12 ± 0.48 | -0.98 ± 0.68 | |
| GLM model | Quasi-Poisson | Quasi-Poisson | Quasi-Poisson | Poisson | Poisson | |
| (L) Coleoptera | | Total adults | P. sericeus | A. sericea | | |
| Brachypodium | 0.11 ± 0.33 | 0.19 ± 0.55 | 0.20 ± 0.45 | | | |
| Stones | -0.40 ± 0.33 | -0.28 ± 0.55 | -1.10 ± 0.52* | | | |
| GLM model | Quasi-Poisson | Quasi-Poisson | Poisson | | | |
| (M) Isopoda | | Total adults | A. arcangelii | | | |
| Brachypodium | -0.74 ± 0.29* | -0.72 ± 0.30* | | | | |
| Stones | -0.25 ± 0.29 | -0.22 ± 0.30 | | | | |
| GLM model | Quasi-Poisson | Quasi-Poisson | | | | |

significantly higher values of cellulose and UEM in the forage (Table 1F). On the contrary, the presence of *B. retusum* shows lower values of Mg, Ca, OM, dMO, dcDM, and UFV (Table 1E–G). In the absence of *B. retusum* and in the presence of stones, values in K, P, protein, and PDIE (Table 1D & 1E) are significantly higher.

On the PCA (Fig. 3) ran on soil, litter, and biomass data, axis 1 distinguishes treatments with *B. retusum* from treatments without *B. retusum*. Treatments with *B. retusum* are characterized by a higher concentration of MgO, carbon, and nitrogen in the soil but also higher values of cellulose in the forage, biomass, and litter mass. Treatments without *B. retusum* show higher values for total protein, digestibility, K, and P in the forage. Axis 2 distinguishes the grassland from treatments on the

abandoned field. It is only characterized by higher values of Na₂O in the soil of the reference grassland.

Vegetation and Bare Ground Covers

Total vegetation cover is significantly higher on the treatments where *B. retusum* was sown and seems to be similar to the vegetation cover of the grassland. Bare ground cover is significantly lower where *B. retusum* was sown (Table 1).

Plant Community Composition and Richness

A total of 66 vascular species have been identified for all treatments. Species richness shows no significant difference

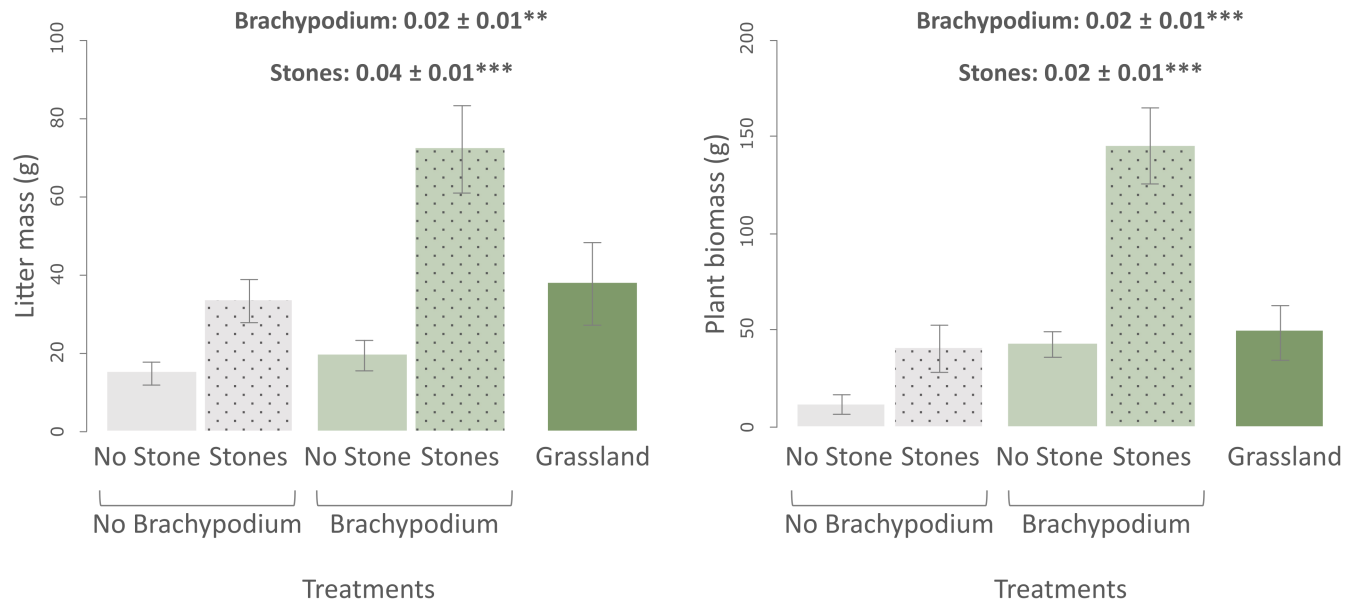


Figure 2. Plant biomass and litter mass. Testing the effect of *Brachypodium retusum* and stones on litter mass and biomass. Parameters were measured on a 1600 cm² sample. Tests were run using Gamma GLM on abandoned field data and grassland means are presented on the right of each graph. The given statistics are estimates (\pm SE), accompanied with stars (**<0.01; ***<0.001). Estimates less than 0.01 were rounded at 0.01.

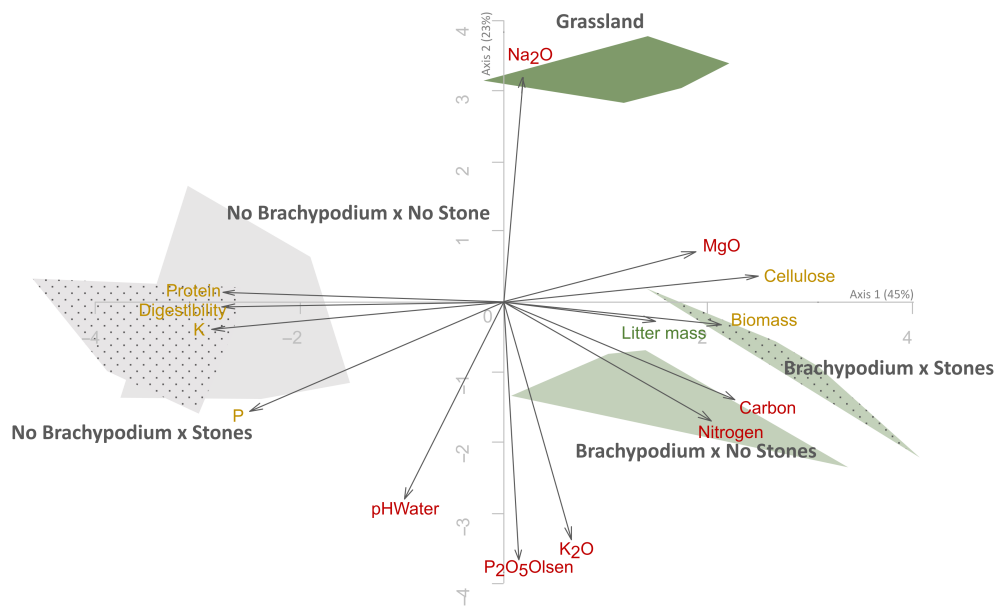


Figure 3. PCA performed on soil, litter and forage parameters for the grassland and the abandoned field. Soil parameters: potassium oxide (K₂O); magnesium oxide (MgO); sodium oxide (Na₂O); available phosphorus (P₂O₅Olsen); total nitrogen (nitrogen, mg/kg); total carbon (C, mg/kg); and pHWater. Forage parameters: cellulose content (cellulose); protein content (protein); contents in phosphorus (P); potassium (K); digestibility of organic matter (digestibility); biomass. Litter mass.

between treatments. Nevertheless, we can note that the mean number of species for each treatment in the restored site (15.3 ± 0.5) is systematically lower than the mean number of species recorded in the grassland (26.6 ± 2.18).

The NMDS on plant community composition is significant (stress: 0.14; $r^2 = 0.42$, $p < 0.001$; Fig. 4) and clearly separates the reference grassland from the treatments on axis 1. The reference grassland is characterized by sub-steppic species, such as

Linum trigynum, *Aira cupaniana*, *Galium parisiense*, and *Hypochaeris glabra*. The composition of treatments where *B. retusum* was sown seems also slightly different from those without. Treatments with *B. retusum* and stones are characterized by more nitrophilous and ruderal species such as *Tragopogon porifolius*, *Hordeum murinum*, *Rubus ulmifolius* (young saplings), *Sonchus oleraceus*, and *Convolvulus arvensis*. Treatments with *B. retusum* but without stone are characterized by annual and

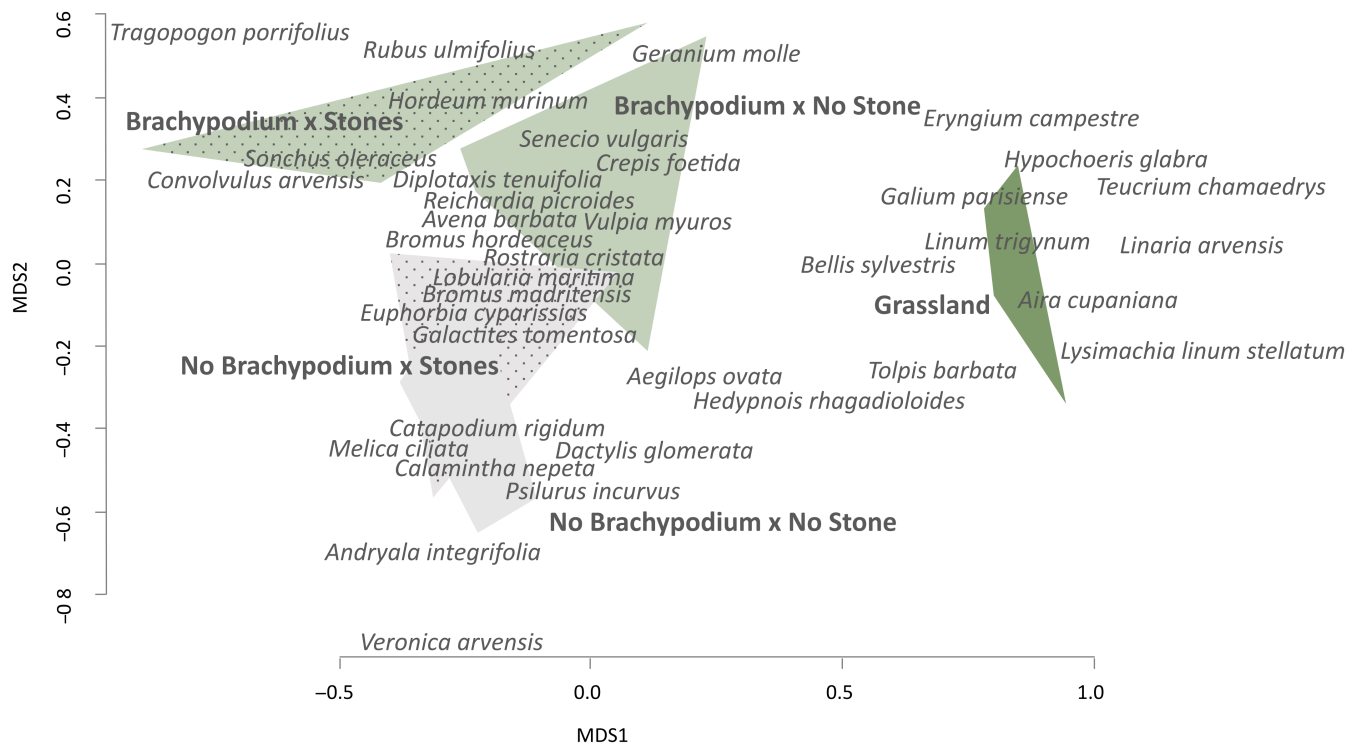


Figure 4. Nonmetrical multidimensional scaling (NMDS) of plant community composition for each treatment. Testing the effect of the presence of *Brachypodium retusum* and stones on plant community composition. The given statistics were run without *B. retusum* and without species present only once on all quadrats. Stress: 0.14; $r^2 = 0.42$.

stress-ruderal species, such as *Geranium molle*, *Senecio vulgaris*, *Crepis foetida*, *Diplotaxis tenuifolia*, *Reichardia picroides*, and *Avena barbata*. Treatments without *B. retusum* whether with or without stones are characterized by the same species: *Galactites tomentosa*, *Catapodium rigidum*, and *Calamintha nepeta* (Fig. 4).

Soil Seed Bank

The species richness of the semi-persistent and persistent seed bank shows no significant difference between treatments. Abundance of seeds in the seed bank is significantly higher with the presence of stones (Table 1H; Fig. 5) and is significantly higher without *B. retusum* (Table 1H; Fig. 5). It can be noted that the species richness of the grassland (9.4 ± 1.5) seems to be the same as for the treatments (8.7 ± 0.51) and that the number of seedlings in the grassland (19.0 ± 3.1) is much lower than in the treatments (47.8 ± 5.2).

The NMDS on seed bank is significant (stress: 0.14; $r^2 = 0.34$, $p < 0.001$; Fig. 6) and clearly separates the reference grassland from the treatments. The seed bank grassland is characterized by characteristic sub-steppic species such as *Poa bulbosa*, *Vulpia myuros*, *G. parisiense*, *Bromus rubens*, *Filago gallica*, *Filago pyramidata*, *A. cupaniana*, *Polycarpon tetraphyllum*, and *Catapodium rigidum*. The composition of treatments where stones were restored is different from those without. Treatments with stones are characterized by ruderal species, such as *D. tenuifolia*, *Euphorbia cyparissias*, *Conyza*

sumatrensis, *Lobularia maritima*, *C. nepeta*, and *Juncus bufonius*, whereas treatments without stones are characterized by annual species such as *Vulpia ciliata*, *Anagallis arvensis*, and *Bromus madritensis* (Fig. 6).

Soil Mesofauna and Arthropods

The number of total Acari, Gamasida, and Oribata is significantly higher with the presence of stones (Fig. 7). On the other hand, epigeous Collembola abundances are significantly lower in the presence of *B. retusum*. The same pattern is observed for isopods (98% composed of *Armadilidium arcangelii*) and for spiders, both for total abundance and for the abundance of *Nomisia exornata* (representing 53% of the total number of individuals). Coleoptera are mainly composed of *Poecilium sericeus* (61%) and show no significant difference between treatments but we can observe more individuals in the grassland (means of 4.3 ± 0.7 for treatments and 9.0 ± 1.9 for grassland). *Asida sericea*, the second most abundant Coleoptera, is found in significantly lower numbers when stones are present.

Discussion

Effects of *Brachypodium retusum* and Stones Restoration on Soil Properties, Forage, and Litter Quality

More than 40 years after the end of the cultivation, the restoration of traditional sheep grazing, and almost 20 years after the

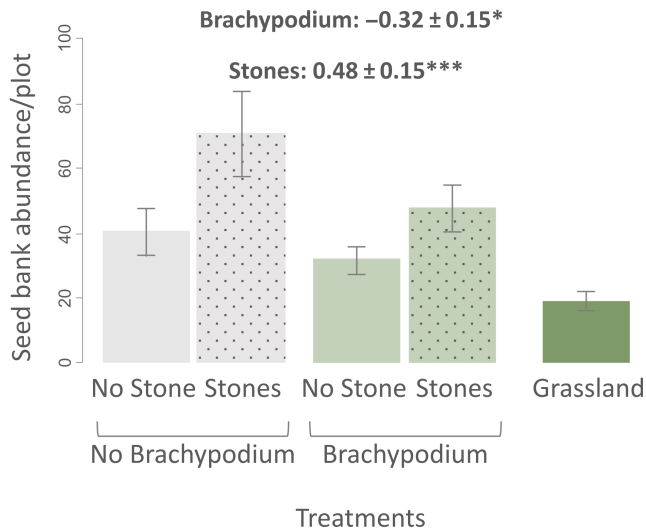


Figure 5. Seed bank abundance for each treatment. Testing the effect of the presence of *Brachypodium retusum* and stones on the seed bank species richness. Parameters were measured on 1 L sample. Tests were run using Quasi-Poisson GLM on abandoned field data and grassland means are presented on the right of the graph. The given statistics are estimates (\pm SE), accompanied with stars (* <0.5 ; *** <0.001). Estimates less than 0.01 were rounded at 0.01.

last experiment (stone cover restoration and *Brachypodium retusum* sowing), soil properties are still very different between the reference grassland soil and the former cultivated field whatever

the restoration treatment. Concentrations of nutrients in the soil are still higher than those of the reference grassland. These high concentrations are consequences of the intensive application of fertilizers in the melon fields and are now well known in this area (Jaunatre et al. 2016, 2023; Helm et al. 2019). High soil pH and higher calcium concentrations measured in the abandoned field are due to deep plowing. It has reached the bedrock at 40 cm deep, bringing back fragments of calcareous conglomerate bedrock into the soil (Buisson & Dutoit 2004).

The reestablishment of the original stone cover in the abandoned field has just led to a slight but significant soil acidification, bringing it closer to the reference grassland ecosystem certainly in relation to an increase in the litter layer and biomass between stones. The reestablishment of *B. retusum* has significant effects, especially on soil parameters. *Brachypodium retusum* treatments lead to higher contents of organic matter and mineral elements in the soil, resulting in highest soil fertility, which drives the restored abandoned field away from the reference grassland with poor soil fertility. Forage analyses reveal lower concentrations of mineral elements (P, K, Mg, and Ca) for *B. retusum* treatments than for treatments without *B. retusum*. However, plant concentrations for these elements are still 10–50 times higher than those measured in the soil regardless of the restoration treatment (with or without *B. retusum*). It therefore seems that *B. retusum*, which is a perennial stress-competitive grass (Grime 1974), is less able to concentrate the remnants of former mineral fertilizers, such as P and K, than the stress-ruderal species of the abandoned field vegetation. This vegetation which characterizes the treatment

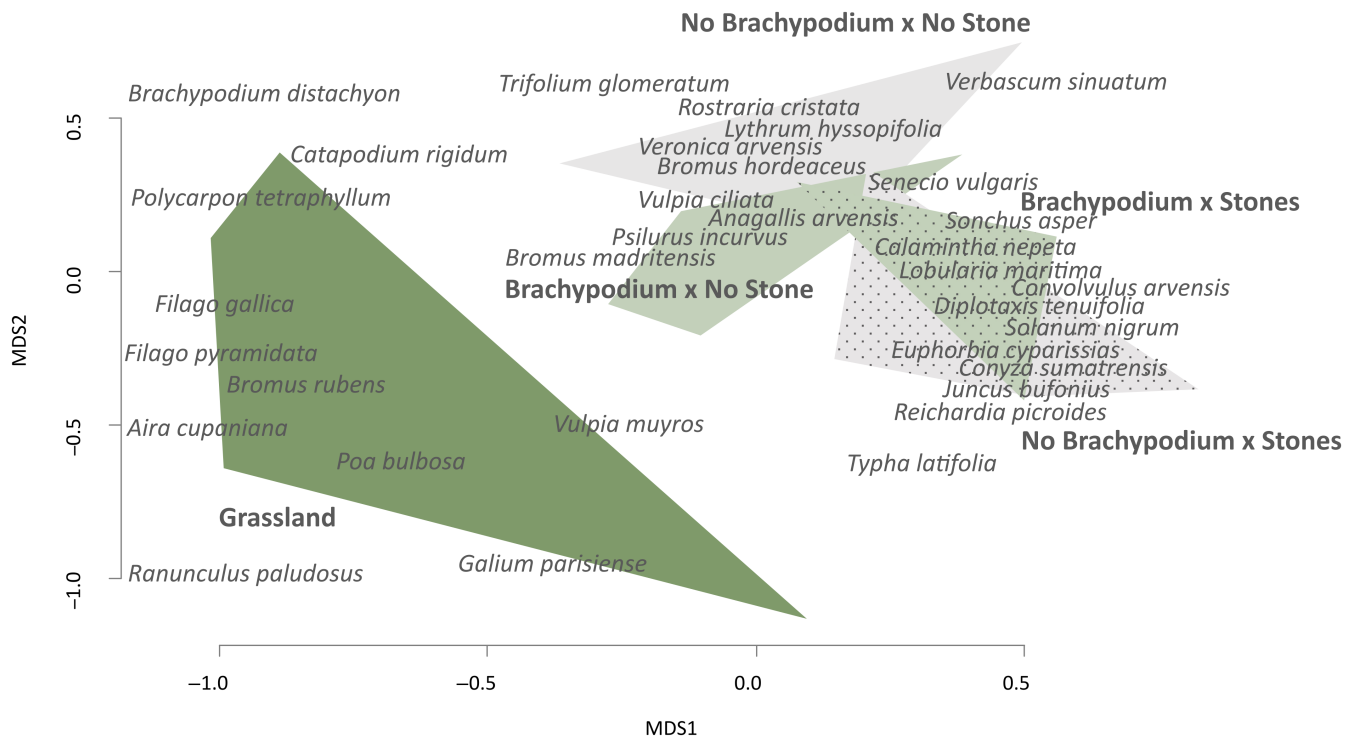


Figure 6. Nonmetrical multidimensional scaling (NMDS) of seed bank composition for each treatment. Testing the effect of the presence of *Brachypodium retusum* and stones on seed bank composition. Stress: 0.14; $r^2 = 0.34$.

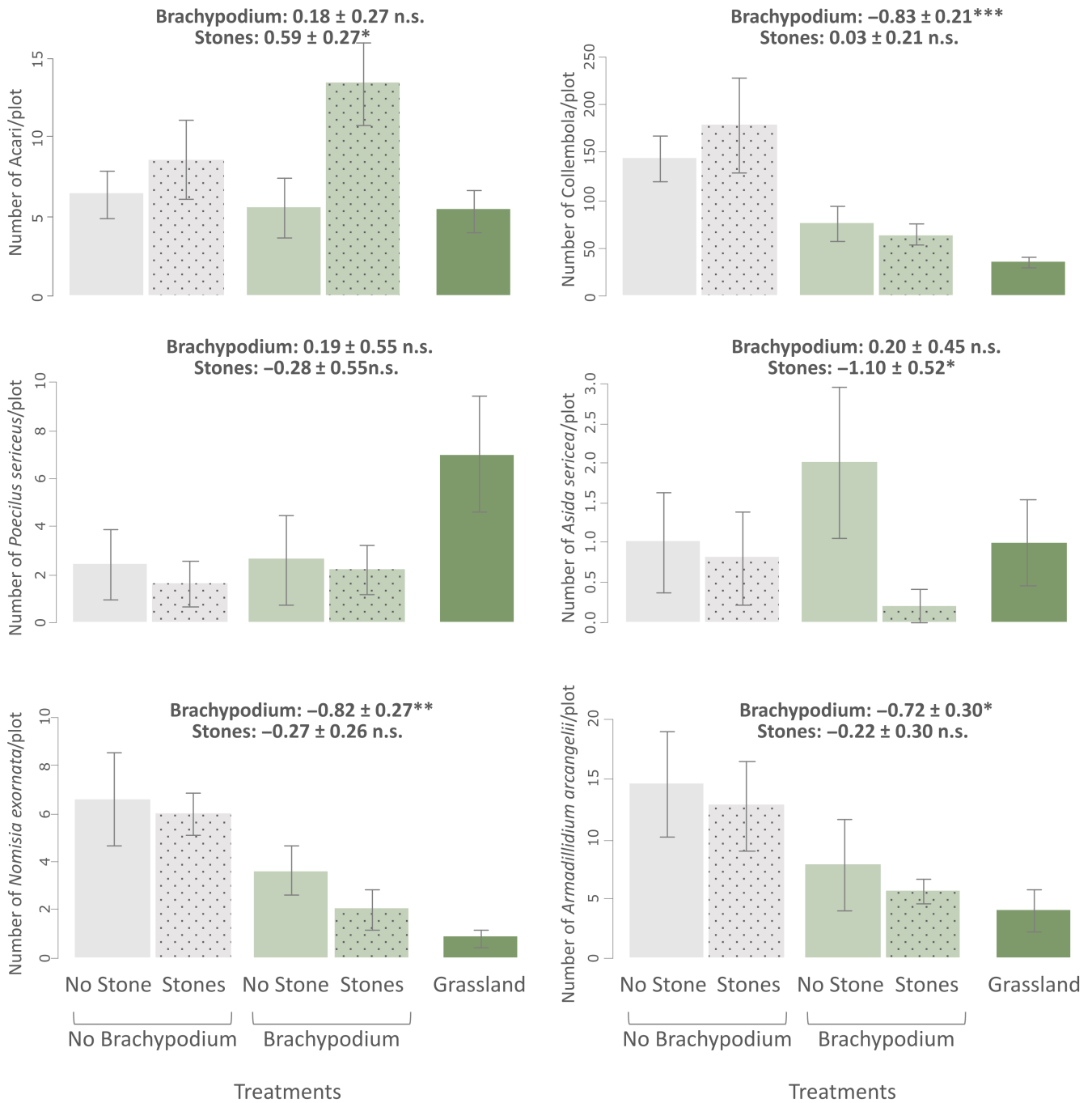


Figure 7. Number of Acari, Collembola, *Poecilus sericeus*, *Asida sericea*, *Nomisia exornata*, and *Amadilidium arcangelii* for each treatment. Testing the effect of the presence of *Brachypodium retusum* and stones. Individuals were captured using pitfall traps except for Acari, captured using Berlese funnels. Tests were run using Quasi-Poisson GLM except for *A. sericea* where tests were run using Poisson GLM. All tests are run on abandoned field data and grassland means are presented on the right of the graph. The given statistics are estimates (\pm SE), accompanied or not with stars (* <0.5 ; ** <0.01 ; *** <0.001). Estimates less than 0.01 were rounded at 0.01.

without *B. retusum* is mainly dominated by some stress-ruderal annual forb species, as previously shown by Helm et al. (2019) and Jaunatre et al. (2023).

The increase in litter mass and biomass with the presence of *B. retusum* can be explained by the fact that it is a less palatable species than the forbs and other grasses of abandoned fields

(Buisson et al. 2015; Vidaller et al. 2022). Furthermore, stones also have a positive effect on the survival of *B. retusum* (Buisson et al. 2015). Bourrelly et al. (1983) has already showed that stones create a microclimate by increasing soil moisture under the stones and allowing the development of above- and belowground biomass in the Crau grassland. We can assume

that stones allow *B. retusum* to protect roots from heat as well as to produce more roots (Ingelmo et al. 1994), which can allow the species to better cope with summer drought. Treatments with *B. retusum* combine low digestibility and a meat fodder unit with lower protein and higher cellulose rates as already shown in other studies (Cingolani et al. 2005; Vidaller et al. 2022). Even after the restoration of the traditional grazing system for decades, we measure a higher biomass for treatments with *B. retusum* in the former cultivated fields. This result is reinforced by the fact that the biomass shows low nutritional and digestibility values, making this plant less palatable, than arable weeds and stress-ruderal species, which dominate in treatments without *B. retusum*.

A research perspective would be to replace the reintroduction of *B. retusum* by another species, such as *Dactylis glomerata* L., a species also present in the grassland flora but with a lower density and cover. We expect *D. glomerata* to have a lower development than *B. retusum* because it is more palatable. Then, it should produce less litter mass and biomass and should allow a better absorption of residual fertilizing elements in the soil (N, P, and K) (Novak 2001).

Responses of Plant Community to *B. retusum* and Stone Cover Restoration

Plant composition is influenced by the presence of *B. retusum* and by the stone cover. It has already been shown that stone cover structures plant community of dry grasslands in this area (Saatkamp et al. 2010; Kumbaric et al. 2012; Buisson et al. 2015). The plant composition of the reference grassland is characterized by typical stress-tolerant species: *Linum trigynum*, *Galium parisiense*, and *Aira cupaniana* (Buisson & Dutoit 2004). Regarding the effects of the different treatments, we can record that the plant composition is structured according to their response to grazing (Vidaller et al. 2022). Treatments with *B. retusum* and stones are characterized by palatable slightly mesophilous species: *Tragopogon porrifolius*, *Hordeum murinum*, and *Convolvulus arvensis*. For this treatment, a high cover of *B. retusum* and the presence of stones provide shelter for plant species to avoid grazing (Devaux et al. 1983). Treatments with *B. retusum* but without sheltering stone are characterized by species less palatable or inaccessible in time (from March to May) or space for sheep (creeping species or in rosettes): *Senecio vulgaris* is already dried in May; *Geranium molle* is a very short species; *Crepis foetida* and *Diplotaxis tenuifolia* have a bitter taste. Treatments without *B. retusum*, with or without stones, are characterized by the same type of species including plants with chemical defenses (*Calamintha nepeta*) or spines (*Galactites tomentosa*).

Effects of *B. retusum* and Stones Restoration on Seed Bank Abundance and Composition

The composition of the seed bank is influenced by the presence of stones. The permanent and semi-permanent soil seed bank of the grassland is characterized by annual grassland stress-tolerant species. Treatments with stones are characterized by slightly more mesophilous species or non-palatable species: *C. arvensis*,

D. tenuifolia, *Sonchus asper*, *C. nepeta*. The abundance of seeds is notably positively influenced by the presence of stones but negatively influenced by the presence of *B. retusum*. Then, the most plausible hypothesis is that seeds from the seed rain slide down the stones surface to concentrate in the space between the stones. The negative impact of *B. retusum* could be explained by the fact that its high cover creates a barrier to the arrival of seeds on the ground and/or its competitive effects on annuals around it (Saatkamp et al. 2010; Génin et al. 2021; Chenot-Lescure et al. 2022). Moreover, as seen previously, *B. retusum* covers the soil with its biomass but also with a significantly higher litter mass, preventing the turnover of the annual species, that is, the germination of annuals from the soil seed bank and the arrival of seeds via the seed rain (Buisson et al. 2006). This result could be interpreted as positive when restoration objectives are to decrease the abundance of former arable weeds that can germinate from the soil seed bank. However, this demonstrates that there is no facilitation effect of *B. retusum* to increase biomass, cover, or species richness of characteristics species of the reference grassland even nearly 20 years after its reintroduction in the former cultivated field. Such results have also been found by Génin et al. (2021) in under-grazed patches of the reference dry grassland dominated by *B. retusum*.

Effects of Stone Cover Restoration on Soil and Ground-Dwelling Arthropods

The positive influence of stone cover restoration on the total abundance of Acari can be explained by the refuge effect of stones, creating a suitable habitat (e.g. higher moisture), and sufficient food resources (Bourrelly et al. 1983). For other taxa (e.g. isopods, epigeous Collembola, and spiders), the positive effect of stones is less clear, suggesting that arthropod responses depend on the soil strata considered. Arthropods living on the soil surface may be less dependent on the micro-habitats created by stones than endogenous species, as they are more resistant to drought. They may use stones as shelters to protect themselves from predators rather than for microclimates that stones create. However, these results could also be partly influenced by the methodology we used. Pitfall traps provide an estimate of the activity-density of arthropods in the plots (Brown & Matthews 2016)—activity-density being the abundance of each species as a reflexion of its activity during the sampling period and the density of the population in the sampled plot. Individual activity is species-dependent and can be modulated by the season, the weather, and the local environment. In particular, trapping potential can decrease as habitats become more complex (Melbourne 1999; Thomas et al. 2006). As a result, pitfall traps placed in stone-covered plots may have a lower trapping potential than traps placed in less complex habitat, masking the low to medium effect of stone restoration. In addition, the range of action of the traps varies according to the species and could exceed the size of our plots for the most mobile ones (Blight et al. 2023). Conversely, sampling arthropods living in the soil is a direct measure of the density of individuals at a specific location, which may better reflect the dependence of arthropods on stones in our small-scale experiment.

We measured no effect, or even negative effects, of *B. retusum* on detritivores, whereas we might have expected higher abundances, particularly of Oribatida. Indeed, they are generally dependent on the structure of the herbaceous plants and the litter mass (Koehler 1999), which is more abundant in the presence of *B. retusum*. As detritivores, Oribatida contribute significantly to decomposition processes and nutrient turnover. Epigeous Collembola are negatively influenced by the presence of *B. retusum* and treatments with higher values of biomass and litter mass. This result may also be surprising, as Collembola are involved in litter decomposition by stimulating the activity of microorganisms and increasing both the mobility and stability of nutrients in terrestrial ecosystems (Hopkin 1997; Rusek 1998; Filser 2002). They are among the best represented groups of soil mesofauna (Rosenberg et al. 2023), in terms of species richness and abundance. However, there is probably no direct link between the abundance of Collembola and litter mass because many Collembola feed on fungus growing on litter and not on litter directly, and also because detrital macrofauna have more pronounced impact on litter mass loss than mesofauna communities (Slade & Riutta 2012). On the other hand, we can suppose that the habitat structure formed by *B. retusum* may be too complex for the mobility of these epigeous individuals. The lack of effects (Oribatida) or the negative effect (Collembola) of *B. retusum* on these two groups may also be due to the low quality of the litter (higher cellulose quantity). This is also the case in the reference grassland, that is, there are few isopods and Collembola in the reference grassland. *Brachypodium retusum* and therefore the structure or quality of the environment might not be suitable to these organisms. The majority of spiders captured were *Nomisia exornata* (Gnaphosidae), a species that potentially predaes ants, Collembola, isopods, and small spiders (Pekár & Jarab 2011; Dušátková et al. 2020). Its presence in the treatments without *B. retusum* can therefore be explained by the higher presence of Collembola and isopods or by a habitat that is too complex for movement and not suitable for hunting. Nevertheless, the treatment that should be closest to the grassland, that is, presence of *B. retusum* and presence of stones, is indeed the treatment closest to the grassland in terms of spider abundance.

At the site scale, as observed in previous studies (Fadda et al. 2007; Blight et al. 2011), the two most abundant Coleoptera species in the grassland are *Poecilus sericeus* and *Asida sericea*, and are also present in the abandoned cultivated field. *Asida sericea* seems to move more than *P. sericeus* (Blight et al. 2023) and could therefore be more widely dispersed. This can explain why *A. sericea* has more or less similar abundances between grassland and abandoned field while *P. sericeus* is less abundant in the abandoned field than in the grassland. Finding high abundances of these two species could be an early indicator of restoration success (Alignan et al. 2018).

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Soil parameters: Detailed description of the methods used to analyze soil physico-chemical parameters.

Supplement S2. Biomass, forage and litter: Detailed description of the methods used to analyze biomass, forage and litter parameters.

Supplement S3. Soil seed bank: Detailed description of the methods used to set up the seed bank in the greenhouse.

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