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Plants playing at home:

Advantage of native plant seeds for ski slope revegetation in the French Pyrenees

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Highlights

- Seeds harvested close to ski slopes can be useful for the restoration of plant cover.
- Local seed mixtures were more efficient than exogenous ones to restore plant cover on the ski slopes.
- The efficiency of revegetation was highly dependent on local soil conditions.

Abstract

Machine levelling for the creation or maintenance of ski slopes is a major source of disturbance in high elevation ecosystems. Traditional, exogenous seed mixtures can help restoring plant cover and mitigate soil erosion, but they comprise species that are not ecologically adapted to high elevation conditions. Here, the use of local seed mixtures, harvested at nearby sites, was compared to that of exogenous seed mixtures for revegetation of three machine-graded ski runs with different soil conditions in the French Pyrenees. The plant cover, biomasses and associated soil microbial activity were recorded for four years following seeding. The results showed that the establishment of the plant cover was highly dependent of the soil conditions and strongly differed between paired plots that had received local or exogenous seed mixtures. In both seed treatments, some Poaceae dominated the plant cover, allowing the settlement of several spontaneous native species. But the plant cover established more rapidly and more densely, and included a larger cover of target, native species after seeding with local compared to exogenous seed mixtures.

1. Introduction

In the Pyrenees, as in many mountain regions, ski resorts and alpine skiing attract millions of visitors, giving them a significant economic value (Pons et al. 2014). Ski run creation for downhill ski is a major source of disturbance in fragile, high-elevation ecosystems (Pintaldi et al. 2017). It often involves machine-levelling of the soil surface to

remove slope irregularities, aiming at lower snowfall requirements and artificial snow production to open the slopes for use. During this levelling, the grading process involves the removal of the original vegetation, topsoil and seed bank (Wipf et al. 2005; Meijer zu Schlochtern et al. 2014), resulting in a severely altered substrate and in the reset of the vegetation succession, (Krautzer et al. 2006; Burt & Rice 2009).

Without intervention, newly created or re-graded ski slopes fail to recover vegetation for many years (Burt & Rice 2009; Roux-Fouillet et al. 2011). In this context, and in order to mitigate the unavoidable erosion of unvegetated soil, active revegetation is the rule. During revegetation, managers must face several challenges. The main concern is the rapid establishment of a dense vegetation cover that will both be ski-compatible, with a low stature herbaceous cover that improves snow cover during the winter months, and mitigate soil erosion, with above 70% ground cover needed to stabilize the top soil (Delgado et al. 2007, Burt 2012). Additionally, the selected plant community must be able to develop on degraded, often compacted soil substrates, to tolerate the harsh high-elevation conditions including high solar radiation and short growing season, and to undergo the continuous disturbance of operating ski slopes (Burt 2012; Meijer zu Schlochtern et al. 2014). Finally, the site managers must increasingly deal with conservation concerns including the maximization of biodiversity, the preservation of aesthetic and attractive landscapes, or sometimes the production of high-quality fodder during summer season. There are some links between these services, with, for instance, a dense plant cover preventing sediment and nutrient runoff, or greater functional diversity of the vegetation being positively related to water and sediment conservation (Pohl et al., 2009; Pérès et al. 2013).

Current erosion-control practices on ski slopes include seeding with commercial mixtures generally dominated by non-native grass and legume species (Burt & Rice 2009), largely recommended by seed companies. However, these mixtures do not always establish successfully even despite high fertilizer inputs (Tsuyuzaki 1995; Krautzer et al. 2006, Burt 2012, Swab et al. 2017), resulting in a poor control of soil erosion. Furthermore, non-native species can generate unintended effects such as the establishment of ruderal woody species (ski slopes are frequently located in forest, with the nearby vegetation including woody species that are undesirable on the slopes), and resistance to the establishment of native, local plant species (Tsuyuzaki 1995; Burt & Rice, 2009; Burt 2012; Barrantes et al., 2013; Hagen et al. 2014), although Hudek et al. (2020) found an increased colonization of native plant species on a ski run in the Italian Alps 17 years after seeding with commercial seed mixtures. Finally, the introduction of exogeneous plant material may lead to genetic evolution of the wild adjacent plants due to hybridization process (Gauthier, 1997).

Local, indigenous herbaceous species may be a relevant alternative to these traditional, exogeneous seeds. They are supposed to be well adapted to the local, climate harsh conditions, and may establish more efficiently, potentially achieving denser vegetation cover (Krautzer et al., 2006; Burt 2012; Swab et al. 2017). Also, many ski resorts are located in protected areas (regional nature parks, or peripheric areas of national parks), where the introduction of exogenous plant material is not desirable or even forbidden by regulations. Although recommended, the use of native seeds for ski slope revegetation is currently not always possible, because local, native seeds are simply not available. Yet, practices using local plant material do exist. Green hay transfer was identified as an efficient practice for reseeding of local species (Scotton et al., 2009; Barrel et al. 2015, Dupin et al., 2019) but can

be achieved on limited surfaces only. The use of a beater brush harvester (Loch et al. 1996) for seed harvesting (or seed stripping) in the surrounding areas provides a promising way to get high amount of diverse, ecologically adapted seed mixtures (Scotton et al., 2009; Durbecq et al. *in prep*). Revegetation with native seeds for restoring grasslands are getting widespread in Europe and elsewhere, including at high-elevation sites. However, their relative effectiveness remains poorly addressed, due to a lack of comparative experimentations and ecological monitoring (Slodowicz et al, 2019). Until now, only a few studies provided accurate dataset about the ecological relevance of these local seeds for revegetation in mountain or under other stressing and disturbed ecological conditions (Scotton 2019; Swab et al. 2017; Scotton 2021). These studies have emphasised the relevancy of native seeds to restore sufficient ground plant cover and species diversity, and to improve soil conservation. In contrast, Barni et al. (2007) found little evidence for re-establishment of native species in ski run seeded with native species compared to exogeneous species 12 years after restoration: in this study, the authors attributed the low success of wild native species to persistent altered soil properties.

The existing literature reports few data about the impact seed material on the plant roots (but see Hudek et al. 2020) nor on the soil microbial community (but see Swab et al. 2017). Yet, plant diversity and soil microbial community are tightly coupled, both explaining ecosystem processes such as soil fertility or stability. For instance, in their study on mountain grasslands, Grigulis et al. (2013) showed an equal contribution of plant and microbial functional parameters in explaining soil organic matter content. Plant and soil microbial parameters both control soil stability (Pérès et al. 2013; Blankinship et al. 2016), with roots stabilizing the soil by mechanical effect, and the finer roots together with soil

microorganisms being the main actors of soil aggregation, which is essential to prevent erosion. The soil microbial community is strongly impacted by the composition of the plant community, mainly because of the amount and biochemical nature of the organic substrates entering the soil as litter and root exudates (Bardgett and Wardle 2010). In turn, an active (and diverse) soil microbial community promote plant establishment and growth by mobilising nutrients, transforming soil organic matter and producing plant growth-promoting substances (Bardgett and Wardle 2010). Also, both plant root inputs and microbial processes contribute to the formation of stable soil organic matter (Sokol et al. 2019; Rossi et al. 2020), then largely contributing to reinstate fertility in degraded soils (Rashid et al. 2016). Because of their contrasted traits, exogeneous species may harbour microbial communities functionally distinct compared to that of their native counterpart (Kourtev et al. 2003), with consequences on soil properties and erodibility.

Here we assessed the interest of using local seeds (compared to commercial, exogenous seed mixtures) on three machine-graded ski runs in the French Pyrenees. Several plant and soil parameters were followed for four years after seeding. We hypothesized that the plant covers from local seed mixture would be denser and more diverse, then providing a better mitigation of soil erosion, compared to plant covers from traditional mixtures. We also hypothesized that soils seeded with native, local seed mixtures would be biologically more active, compared to soils seeded with exogenous mixture, because of a higher plant cover and root colonization.

2- Material and Methods

2.1- Study sites and assays

The study was carried out in three ski resorts of the Pyrenees, South of France, on ski slopes that were recently submitted to levelling operations. The three experimental sites were selected for their contrasted soil characteristics: Font Romeu (with rather rich topsoil conditions), Grand Tourmalet (with intermediate topsoil conditions) and Les Angles (with poor soil conditions) (**Table 1**, **Supplementary material S1**). At Les Angles, the local substrate was graded to remove the largest rocks, while at Font Romeu and Grand Tourmalet, topsoil from nearby sites was spread on the slopes after grading. Composite soil samples (five soil cores) were collected at each site, and soil parameters were analysed by the Laboratory for Soil Analyses (INRAE Arras, France). The topsoil parameters for the three sites are presented in **Table 1**.

As for many experimental studies on ski runs, no experimental replicate could be established because of the technical constraints of seeding practices that include the use of an hydroseeder. Thus, for each site, one plot received a mixture of commercial, exogeneous seeds (ES) while another adjacent plot with similar conditions of soil, slope and exposition received a mixture of local seeds (LS) that were harvested at nearby sites using a beater brush harvester (Logic MSH 420).

The exogenous commercial seed mixture at Font Romeu (Pyrénées versant Sud, Company Gazon de France, France) was composed of *Schedonorus arundinaceus* (20%), *Festuca*

rubra (25%), *Phleum pratense* (15%), *Lolium perenne* (15%), *Dactylis glomerata* (15%), *Lotus corniculatus* (5%), *Trifolium repens* var Huia (4%), and *Achillea millefolium* (1%).

The exogeneous commercial seed mixture at Grand Tourmalet and Les Angles (mixture Pyrénées Sud, company Gazon de France, France) was: *Schedonorus arundinaceus* (20%), *Festuca rubra* (25%), *Dactylis glomerata* (15%), *Lolium perenne* (15%), *Onobrychis viciifolia* (5%), *Poterium sanguisorba* (3%), *Phleum pratense* (13%), *Plantago lanceolata* (1%) *Trifolium repens* var Huia (2%) *Achillea millefolium* (1%).

Local seeds at Font Romeu and Les Angles were yielded from former hay meadow (elevation 1690 m), with *Festuca nigrescens* (60.73% final mass), *Nardus stricta* (2.60%), *Koeleria pyramidata* (3.64%), *Briza media* (1.51%)*Ranunculus acris* (1.30%), *Carex brizoides* (1.20%), *Anthoxanthum odoratum* (1.10%), *Rhinanthus minor* (0.74%), *Bistorta officinalis* (0.60%), *Galium verum* (0.30%), *Scorzoneroides pyreanica* (0.30%), *Trifolium pratense* (0.30%), *Carex nigra* (0.20%), *Conopodium majus* (0.20%), *Plantago lanceolata* (0.10%), *Vicia sepium* (0.10%), *Dianthus deltoides* (0.01%), *Taraxacum sp.* (0.01%), *Tragopogon pratensis* (0.01%), *Achillea millefolium* (6.20%), *Dactylis glomerata* (1.60%), *Poa trivialis* (1.05%), *Phleum pratense* (0.80%), *Poterium sanguisorba* (0.10%). *Trifolium repens* (10.30%) and *Lolium perenne* (5.0%) from exogenous origin were added as 'nurse' species to this mixture.

Local seeds at Grand Tourmalet came from a nearby subalpine grassland (*Nardion strictae*, elevation 1930 m) with *Festuca nigrescens* (79.10%), *Nardus stricta* (5.30%), *Festuca eskia* (4.10%), *Briza media* (1.20%), *Avenella flexuosa* (2.30%), *Poa alpina* (1.20%), *Dianthus deltoides* (0.70%), *Carex nigra* (0.3%), *Galium verum* (0.20%), *Conopodium majus* (0.18%), Jasione laevis (0.30%) , *Plantago monosperma* (0.20%), *Achillea millefolium* (3.00%), *Lotus*

corniculatus (0.02%). Additional seeds of local *Trifolium repens* (yielded using a beater brush hartvester at a nearby site) were added to the mixture as nurse species (1.90%).

The application conditions of seed mixtures (including the use of fertilizers, hydromulch of wood fibers and vegetal colloids) are presented in **Table 1**. There are little differences in sowing densities that may not have influenced our results as Scotton (2019) showed that in coarse or high-altitude soils, plant density is not dependent on the sowing density. The assays were established in the fall 2014 (for Grand Tourmalet site) or 2015 (for Font Romeu and Les Angles sites) and monitored during the initial four years of establishment during the summer season (noted Y1, Y2, Y3 Y4) to characterize the success of exogeneous (ES) and local seeds (LS).

2.2- Vegetation survey

In each plot (corresponding to each seeding treatment at a given site), ten sampling areas, distributed within the plot (**Supplementary material S2a**) were flagged with staples planted into the soil parallel to the slope direction. Quadrats of a 0.5 x 0.5 m each comprising twenty-five 0.1 x 0.1 m squares were positioned on the sampling area using the fixed staples. The percent covers (average surface cover per quadrat, with an accuracy of a quarter of square *i.e.* 1 % of the quadrat surface or 25 cm²) were recorded for live vegetation, fine earth (< 2 mm), small (< 10 mm), coarse gravels (> 10 mm,) and others (moss or wood debris).

For botanical surveys, each species present in the quadrats was recorded, as well as its relative cover (percent cover). Species percentage frequencies were recorded for each quadrat as the number of squares in which a species was found divided by the total number

of squares (*i.e.* 25) for Poaceae, that were dominant in the plant cover. The species richness was noted at the plot level as the total number of species present across the ten quadrats in the plot. The recorded species were classified by their typical habitat (subalpine grassland, meadow, stony and sandy habitat, peatland and outlet, heatland, forest) according to the Baseflor database (Julve 2020) and also as 'forage' or 'non-forage' species following Daget & Poissonet (1969) and Jouglet (1999).

2.3- Plant biomass and soil sampling

Plant above- and belowground parts and associated soil were sampled in four additional quadrats using four squares for each quadrat, *i.e.* 0.04 m² (**Supplementary material S2b**). The above-ground plant parts were carefully yielded using scissor. In the same four squares, the soil including root parts was yielded with a soil corer (0.04 m diameter, 0.1 m depth). When the presence of stones prevented from digging, the soil core was collected in an adjacent square. Aboveground parts and soil cores from the 4 squares of a given quadrat were pooled together to get four composite samples (4 plant aboveground samples and 4 belowground soil and root samples for each plot). The roots were carefully sorted, removing gravel and dead material. Aboveground vegetation and root materials were rinsed with deionized water to remove adhering soil, oven-dried at 65°C until constant mass and weighed. The records of aboveground and belowground dry biomasses were further converted in $g \cdot m^{-2}$.

2.4- Soil microbial activity

Substrate induced respiration (SIR) was determined as a proxy of the soil microbial biomass and activity (Nannipieri et al. 2003) according to Beare et al. (1990). Briefly, 20 g air-dried 2-mm sieved soil samples were incubated in 150 mL sealed serum flasks at 80% field capacity with 1.5 mg C-glucose g^{-1} soil and at 25°C; two-hundred µL air samples from the headspace were analysed after 2 and 6 hours for CO_2 concentration in the flasks using a microcatharometer (MicroGC serie S, SRA Industries, Marcy l'Etoile, France) equipped with a PoraPlot column (Agilent, Santa Clara, United States). SIR rates were calculated as the mass of C-glucose converted to C-CO_2 per g of soil DW and per hour (µg C-CO_2 g^{-1} soil h^{-1}).

2.5- Data analysis

Vegetation and microbial data were analysed with XL-STAT 2017 and R version 3.2.2. Because the data were collected in unique, experimental plots per treatment at each ski slope (site), the quadrats could not be used as true replicates. To deal with this issue, the effect of local *vs* exogenous seed mixtures on vegetation percent covers was tested across the three experimental sites and the four sampling dates using mixed models with repeated measures. The site (ski slope) was used as random factor and the interaction between site and seed mixture effect was interpreted as the specific site effect. The normal distribution of residuals was verified using a Shapiro-Wilk test ($\alpha = 0.05$).

Plant cover, above- and below-ground biomasses, and SIR rates were compared between local and exogeneous seeds at each sampling date using Mann-Whitney tests ($\alpha = 0.05$). Non-

metric multidimensional scaling (NMSD) ordination was used to visualize the vegetation composition temporal dynamics across the three sites and seed mixture treatments, based on the composition of the plant community (contribution of plant species to the total plot vegetation cover averaged across the ten quadrats) from the three (Grand Tourmalet) or four (Font Romeu, Les Angles) sampling years. Cover values of plant species were log-transformed ($\log10(D + 1)$) before analysis to reduce the weight of abundant species. Bray-Curtis dissimilarity matrices were used and the NMDS was performed using 500 iterations.

3- Results

3.1. Plant cover dynamics

Plant cover (expressed as quadrat surface percent cover), globally increased with time for both local and exogeneous seeds, with strong differences between sites and seed mixtures, and generally tended to reach a plateau after 3 years (**Figure 1a**). Total plant cover was consistently higher with local (LS) compared to exogeneous (ES) seed mixtures (mixed models with repeated measures, F = 13.534, p = 0.021, Tukey test), and with no significant interaction effect between site and seed mixture factors (Z = 0.957, p = 0.169), denoting that seed mixtures had a consistent positive on the plant cover across the three sites.

At Font Romeu, the plant cover rapidly developed in the local seed plot, with more than 50 % covering after the first growing season and reaching 88 and 91 % cover after 3 and 4 years, respectively. Seedlings from exogeneous seeds suffered following a severe freezing

period that occurred during the first weeks after seedling, with less than 20 % cover after one year. Plant cover in ES plot then rapidly developed to reach 70-80% after 3 growing seasons (Y3) but tended to decrease at Y4 following drought conditions and erosion (see below). On average, plant cover was 1.7-fold higher (across the 4 sampling dates) with local compared to exogeneous seed treatments. At Grand Tourmalet site, vegetated cover from LS mixture was consistently higher compared to that from ES mixture (**Figure 1a**). Plants from local seed mixture rapidly established to reach 60 % cover after two growing seasons and 80 % after 3 and 4 years, while plants from the exogeneous seed mixture, plants hardly settled, reaching 32.8 % average cover at Y4. Average plant cover was more than 2 times higher across the four sampling years with LS compared to ES mixtures. At Les Angles, total plant percentage cover remained low (22.2 and 15.5 % vegetated cover at Y4 for LS and ES, respectively). Despite this bad growth, total plant cover was about twice higher in local compared to exogeneous seed plots (**Figure 1a**).

A higher percentage frequency was recorded for Poaceae, that dominated the plant cover, in LS compared to ES plot (**Supplementary material S3a**). This indicated a more regular distribution of *Poaceae* in LS compared to ES plots at the three sites (**Supplementary material S3b**).

These differences in plant cover following the use of local or exogenous seed mixtures were also visible in terms of percent surface covered by fine earth, and coarse elements (stones) that resulted from both absence of vegetation cover and removal (by erosion) of fine soil particles (**Supplementary material S4).** Indeed, the proportion (percent cover) of coarse (>10 mm) elements was consistently 2.5 to 3 times higher with the use of exogeneous seeds compared to that of local seeds. This was particularly critical at the Grand Tourmalet site. In

ES plots, erosion occurred actively, and the depth of gullies rapidly exceeded 0,15 m depth, resulting in huge soil losses (see **Supplementary material S6**).

3.2. Plant above and belowground biomasses

Total above- and belowground plant biomasses also differed to some extent between LS and ES treatments across the three sites (**Figure 1b**). At Font Romeu, above and belowground plant biomasses were higher with local compared to exogenous seed mixtures but after one growing season only. At Grand Tourmalet, patterns for aboveground and root biomasses were quite similar with consistently higher aboveground and root biomasses after 2 (aboveground only), 3 and 4 growing seasons. Finally at Les Angles, higher belowground biomasses were also recorded with local seed mixture after 2 and 3 years but did not differ after 4 years.

3.3. Plant community structure and diversity

A total of 75 plant species was recorded across all sites and sampling dates, including some species present in the initial seed mixtures (**Supplementary material S5**).

In terms of species richness, the total number of plant species recorded in plots across the two seed mixture treatments and four sampling years ranged from 12 (at Les Angles for ES-Y2 and LS Y3-Y4) to 33 species (Font Romeu ES-Y3). Total species richness (averaged across the three to four sampling years) was 25.2 and 26.8 and in LS and ES plots,

respectively, in Font Romeu, 19.3 and 16 in Grand Tourmalet, and 13.5 and 13.3 in Les Angles (**Table 3**, see details in **Supplementary material S5)**). The number of species that were present in the initial seed mixtures and that were recorded in the plots ranged from 5.8 to 8 on average (among the 10 to 26 seeded species present in the mixtures). Finally, numerous species recorded in the plots (45 to 78% of total species richness) were growing spontaneously, *i.e.* were not present in the seed mixtures, for both LS and ES plots (**Table 3**).

3.4- Species composition :

The plots that had received local or exogenous seed mixtures exhibited strong difference in plant composition across the three sites, and with a stronger site effect compared to the sampling date effect (**Figure 2**, **Supplementary material S5**). Globally, the composition of the plant cover strongly differed between LS (lower part of the NMDS plot) and ES plots (top of NMDS plot, **Figure 2**). The composition of the plant covers fitted to some extent that of the corresponding seed mixture especially at Les Angles and Grand Tourmalet, but to a lower extent at Font Romeu. The plant community composition differed more in Font Romeu (on the right of NMDS plot) compared to Les Angles / Grand Tourmalet where they were more similar to each other (on the left). While some species were present at all sites in both LS and ES plots (*Achillea millefolium*, *Agrostis capillaris*, *Atocion rupestre*, *Dactylis glomerata*, *Festuca eskia.*, *Lolium perenne*, *Murbeckiella pinnatifida*, *Spergularia rubra*), other species were recorded only in LS plots (*Festuca nigrescens*, accounting for 53.6 to 91.0% of the total plant cover), or in ES plots (*Festuca rubra*, with up to 77,7% plant cover,

Phleum pratense Schedonorus arundinaceus), all present in seed mixtures. Some species were recorded in one site only (*Coincya monensis*, *Cytisus oromediterraneus*, *Meum athamanticum*, *Plantago maritima*, *Platago monosperma*, *Scleranthus perennis*, *Scorzoneroides pyrenaica*, in Font Romeu, *Gnaphalium sylvaticum*, *Jasione laevis*, *Ranunculus pyrenaeus* at Grand Tourmalet, and *Cirsium eriophorum*, *Hypochaeris radicata*, *Sisymbrium austriacum* at Les Angles): these species were generally spontaneous (*i.e.* not present in the seed mixtures). Other species were recorded at two sites only (*Crocus nudiflorus*, *Nardus stricta*, *Paronychia polygonifolia*, *Trifolium alpinum*, and *Veronica fruticans* missing at Les Angles, *Pilosella lactucella* and *Rumex acetosella* missing at Grand Tourmalet, *Plantago lanceolata* and *Trifolium repens* missing at Font Romeu).

Across the three sites, several species that were present in the seed mixtures failed to establish in the plant cover in any of the three plots where they were seeded and whatever their proportion in the initial seed mixtures. This was the case for: *Carex nigra*, *Conopodium majus*, *Dianthus deltoides*, *Galium verum* in LS mixtures, and for *Onobrychis viciifolia* (although present in large proportion, 5-10% of seed mixtures) in ES mixtures. Conversely, some seeded species were recovered in all the plots where they were seeded, including *Achillea millefolium*, *Dactylis glomerata* (in LS and ES plots), *Festuca rubra* and *Schedonorcus arundinaceus* (in ES plots) and *Festuca nigrescens* (in LS plots), as well as others that were seeded in one or two sites. Finally, a large number of species were spontaneous, *i.e.* recorded in the plots although not present in the seed mixtures, in both LS and ES plots. Most of these spontaneous species are characteristic of subalpine grassland or stony/sandy habitats (**Table 2**, **Supplementary Table S5**).

In terms of origin of plant species, a larger proportion of plant cover came from seeded species in LS compared to ES plots, especially at Font Romeu where a large proportion of ES plant cover corresponded to spontaneous species (especially *Agrostis capillaris* that accounted for 45 to 65.6% of plant cover across the sampling dates) (**Figure 3a**). Finally, the two meadow species that were added to the local seed mixture were not always successfully recovered in the plots they were seeded in: at Font Romeu, *L. perenne* rapidly disappeared after the second year while *T. repens* failed to establish despite its high proportion in the LS mixture (**Supplementary material S5)**.

3.5- Plant cover composition by habitat type, forage value and species origin

The composition of the plant covers differed between plots seeded with exogenous and local seed mixture also in terms of plant cover by habitat types (**Figure 3a**, plant cover composition after 4 years).

At Font Romeu, with high plant covers, species from subalpine grasslands represented 94.3 % of the plant cover in LS plot, while ES plot cover included 53.5% of species from subalpine grasslands, 36.9% of species from meadows as well as 7.3% of species from stony or sandy habitats (**Figure 3a**, **Supplementary material S5**): the percent cover of species from subalpine grassland was higher in LS compared to ES ($p < 0.001$, Mann Whitney test). At Grand Tourmalet, plant cover in LS plot was largely composed of species from subalpine grasslands (94.9% of the plant cover) while the plant cover in ES plot was dominated by species from meadow habitat (89.5%). At Les Angles, with low total plant cover even after four years, the cover proportion of species from subalpine grassland was

56.8% in LS compared to 13.1% in ES plot ($p < 0.001$). The large cover proportion of species from meadows recorded in ES plots did not differ, however from that of LS plot (41.7 and 85.1% in LS and ES, respectively, $p = 0.109$) because of the large heterogeneity of plant cover.

In all plots, the established plant covers after four years were mainly composed by species of good fodder value (with proportions of vegetation cover between 77.9% in Grand Tourmalet LS, to 97.9% at Les Angles LS, **Figure 3b**). The percent cover of fodder species (on total plant cover) was higher in LS compared to ES plots at Font Romeu ($p < 0.001$) and Les Angles ($p = 0.029$), but not at Grand Tourmalet ($p = 0.052$).

Finally, the plant cover was analysed in terms of proportions of species issued from seed mixtures or of species that were not present in the seed mixtures, qualified here as 'spontaneous' species. The species recorded in the covers were predominantly from seeded species (relative cover by seeded species ranging from 83.5% in Les Angles ES to 97.9% of vegetation cover at Les Angles ES), except for the ES plot at Font Romeu for which the vegetation cover was dominated by *Agrostis capillaris* (45 to 66% across the years) which was not present in any of the seed mixtures (**Figure 3b**). Also, the proportion of plant cover from seeded species was consistently higher in plots with local seed mixtures compared to those with exogenous seeds (Mann Withney tests, $p < 0.001$, $p = 0.004$ and $p = 0.029$ at Font Romeu, Grand Tourmalet and Les Angles, respectively).

3.6- Soil microbial activity

Soil SIR rates differed between the three sites, with highest values at Grand Tourmalet site with local seed mixtures (11.05 µg CO_2-C g^{-1} soil h^{-1} on average across the four years), and lowest at Les Angles with exogenous seed mixture (1.91 µg CO_2-C g^{-1} soil h^{-1}). A significant effect of seed mixture was evidenced at Grand Tourmalet site only, with higher SIR rates with local compared to exogenous seed mixture 2, 3 and 4 years after seeding (**Figure 1c**). At Font Romeu and Les Angles, soil microbial activity (SIR) was comparable in the plots with local and **exogenous** seed mixtures.

4- Discussion

Across assays in three sites with different soil conditions, when seeding graded ski slopes with seed mixtures from local plants (collected nearby with a beater brush harvester) or from exogenous species, contrasted plant covers were recorded, at least during the four years following seeding. Plant cover in the plots treated with local seed mixtures developed more densely, especially at the sites with rich and intermediate soil conditions, reaching over 70% cover after the second year. The lower plant (especially Poaceae) cover rapidly resulted in the loss of fine earth and the formation of gullies that are not favourable to plant growth, worsening the erosion process. However, gullying can sometimes favour the establishment of species from stony habitats, for which the seeds can be carried by runoff water, and that can hang on the edge of the gully, at least temporarily (**Supplementary material S6**).

The higher plant cover recorded in LS plots can be explained by an improved survival of seedlings from native species rather than by their higher biomass. Indeed, the higher plant

cover in LS compared to ES plots did not always translate into higher plant biomass (except at Grand Tourmalet). This is probably because high-elevation plants have low stature and slow growth, compared to exogenous meadow species that are generally selected for their high biomass production and fast growth. High-elevation herbaceous plants also display functional traits that differ among species: they are generally smaller (Wright et al. 2017), grow slowly because of the lower reserve in the seeds, and display thicker leaves and denser tissues (Midono et al. 2019) compared to plants from lower elevation sites, probably in response to low temperature and high irradiance. Both plant aerial parts, that protects the soil surface against raindrop impact and surface run-off, and roots, that trap sediments and favour infiltration, contribute to preventing soil erosion (Stokes et al. 2014, Vannopen et al. 2015). LS plots were largely dominated by the tussock grass *Festuca nigrescens* (that accounted for 53.6 to 91.0 % of the plant cover according to sites and years), while ES plots were largely dominated by *Festuca rubra*. These two graminoids largely contribute to soil aggregate stability with their dense root system (Hudek et al. 2017). *Festuca nigescens*, that is naturally occurring sparsely in subalpine grasslands, is particularly appropriate for ski slopes and their recreation operative conditions, with its low stature that stabilize the snowpack. However, it was not easy to differentiate between *Festuca* species (especially between *F. nigrescens* and *F. rubra* that look very similar). In the plots seeded with exogenous mixtures, part of the plants recorded as *Festuca rubra* might be actually *Festuca nigrescens* that grows spontaneously.

The higher plant cover in LS compared to ES plot did not translate into higher soil microbial activity, except at Grand Tourmalet (**Figure 1c**) where higher soil microbial

activity correlated to higher above- and belowground biomasses in LS compared to ES plots. This result is in line with Swab et al. (2017) showing that the β-glucosidase soil microbial activity was sometimes lower and sometimes higher in areas planted with native compared to traditional seed mixtures in reclaimed mine lands. In line, Gros et al. (2004), working along a restoration chronosequence of restored alpine grasslands, showed that the soil microbial community was very unstable during the years following ski run restoration, probably because of the strong disturbance following ski run grading. Other factors than seeding types may influence the soil microbial activity, such as nutrient availability: competitive interactions between the plant and the soil microbial community could explain the contrasting responses of the soil microbial activity (SIR) across the three experimental sites.

Besides denser covers, the plots seeded with local seed mixtures also exhibited a plant cover different from that of the plots that received exogenous, commercial seed mixtures. Plant species richness was generally comparable in the plots seeded with exogenous or local species seed mixtures at a given site (**Table 3**). Seeded species accounted for 20 to 50% of the number of species recorded in the plots, indicating that a large proportion of species were spontaneous, especially in ES plots with more than 50% of the recorded species on average (**Table 3**), including species that were present at the nearby natural sites (*e.g. Agrostis capillaris* or *Poa alpina*). Some species such as *Achilleum millefolium*, *Plantago lanceolata*, and *Trifolium repens* recorded in the plot covers could be either spontaneous or seeded, although the observation of spontaneous plant cover developing in an unseeded plot at Font Romeu (data not shown) advocates for a spontaneous colonization of these species. The large proportion of spontaneous species, generally from subalpine grassland or stony habitats, suggest that the use of exogenous species in the seed mixtures does not prevent these species

from establishing, in line with recent studies. Hudek et al. (2020) showed that the use of traditional exogenous seed mixture can be efficient for the restoration of graded ski slopes, compared to paired, undisturbed control sites, with species richness after decades being comparable in seeded slope and undisturbed vegetation. Also, Scotton (2021) showed that sowing with forage plant cultivars did not prevent the native species from close natural ecosystems efficiently to establish. In contrast, Hagen et al. (2014) showed that native vegetation cover and species richness were higher in unseeded sites compared to sites with commercial seeds 21 years after seeding in an alpine firing range in Norway. In the present study, at Les Angles and Grand Tourmalet, spontaneous desired species hardly settled in the plots that had received exogenous seed mixtures, despite the growth of *Festuca rubra* that could have facilitated their establishment ('nurse' effect). This is probably because of bad soil conditions following erosion in the ES plots. Alternatively, these data suggest that both the seeded local *F. nigrescens* and exogenous *F. rubra*, that grew densely, could dampen the establishment of a diverse cover with native plant species, at least during the first years after seeding. It could be interesting to monitor the plant succession on a longer term at the study sites to see if a more representative and well-balanced vegetation can settle when some of the first established plants will disappear. The botanical survey for four years showed, however, very few changes in the composition of the plant community in a given plot from one year to the next, especially regarding the spontaneous species (to a lower extent at Les Angles). This result could either suggest that these species were already present at the time of sowing in the soil seed bank and established rapidly, or may be favoured by the local conditions (seedlings resistant to poor soil condition erosion, species selected by summer grazing…). Finally, because of thicker and late melting snowpack (*e.g.* Allegreza et al. 2017),

and of the artificial snow that can provide additional nutrients (*e.g*. Bacchiocchi et al. 2019), the soil conditions differ on ski slopes compared to the nearby slope sites, so that the purpose of restoring a plant cover similar to that of the surrounding alpine grasslands may be not realistic.

Pohl et al (2012), working on machine-graded ski slopes in the Alps, showed that soil aggregate stability increased with plant species richness in highly disturbed soils such as graded ski slopes. The present data suggest that local seed mixtures, although not more diverse in terms of species number, were more efficient in restoring plant cover and protecting the soil from erosion, as compared to that using exogenous seeds, primarily because of a larger plant cover. The plant species diversity translates into diversity of plant functional types (growth forms) and traits (rooting types), that could be important as well for the control of soil erosion (Pohl et al. 2012; Reubens et al. 2007). The ability of plant species to be effective in slope soil restoration could be explained by a trade-off between traits involved in productivity (competitive-ruderal strategy) and resistance to harsh conditions and erosion (Bochet & Garcia-Fayos 2015).

Despite plant species richness that was similar to that of ES plots, the plots restored with native local seeds were more representative of the plant communities naturally occurring in subalpine grasslands on acid soil in the Pyrenees (**Figure 3a**). The natural and dense nearby grassland habitats are dominated by the grasses *Festuca eskia* and *Nardus stricta*, often associated with *Trifolium alpinum*, and *Agrostis capillaris*, that are adapted to cold climate and poor soil conditions, all recorded as spontaneous in both LS and ES plots. Conversely, the cover of the plots seeded with exogenous seed mixtures was dominated by

species from low-elevation meadows (**Figure 3**a), that may be badly adapted to high elevation conditions. Among them, the two exogenous *T. repens* and *L. perenne* added as 'nurse' species to the LS mixture at Font Romeu and Les Angles failed to establish in significant proportion, as they suffered from early frost occurring during the first autumn. The vegetation dynamics recorded in the experimental plots suggests that some species are useless in seed mixtures (e.g. *Carex nigra*, *Onobrychis viciifolia*) while others, even being non-native (e.g. *Festuca rubra*, *Lolium perenne*) can play a 'nurse' role, favouring the establishment of other, more demanding species. The present data also suggest that the composition of the seed mixture shall account for the local site specificities (geological substrate, exposition), as some species were successful at Les Angles and unsuccessful at Font Romeu (e.g. *Plantago lanceolata*, *Trifolium repens*), and vice et versa, with these two sites being distant by about 10 km.

The use of local seed mixture also provided a higher forage plant cover compared to that of exogenous seeds. *F. nigrescens*, that largely dominated the plant cover in LS plots, is a good forage species with high productivity, as compared to other species from high-elevation sites and/or to species that are conventionally used in revegetation. This is important because the use of traditional, exogenous seed mixtures on ski runs generally strongly decrease the pastoral value compared to non-disturbed grasslands (Barrantes et al., 2013).

Finally, the results also highlight the key role of soil initial properties and erosion susceptibility. On very degraded soil such as at Les Angles, sowing with either local or exogenous seed mixtures, and using traditional practices that include the use of fertilizer and

fixator, was not effective to restore a sufficient plant cover. Other promising restoration practices include the use of mulch collected on nearby hay meadows (Durbecq et al. *in prep*), and of wood fibres or adjuvants that are commonly employed in hydromulching practices aiming at protecting the soil from erosion process. Organic fertilizers (*e.g.* manure) can also be used, aiming at fostering a sufficient plant growth, as suggested by other assays (B. Dupin, unpublished). Soil slope and fertility and climatic conditions must be taken into account to adapt revegetation practices. As suggested by other studies, it is also important to consider seed mixture composition according to plant requirements and local prevailing environmental filter (Scotton 2019, Bochet & Garcia-Fayos 2015). Because the restoration of soil might be much longer than that of the plant cover (Hudek et al. 2020), we suggest, as for plant survey, longer-term monitoring of soil properties to better understand the role of the seed mixture.

Conclusions

Working on three ski slopes with contrasted soil properties, the use of local seed mixtures was more effective in restoring a dense and ecologically adapted plant cover, compared to the use of traditional seed mixtures with exogenous species selected from low elevation meadows. The botanical surveys clearly evidenced that both local and exogenous seed mixtures allow the establishment of several spontaneous species (although in low proportion of the plant cover) and that both seeded and spontaneous species coexist. However, after four years, the composition of the plant cover in the plots seeded with local species was closer to

that of subalpine grasslands and with a higher forage value. These data also suggest that achieving simultaneously a dense (for soil erosion control) and species-diverse plant cover is challenging, with some seeded or spontaneous Poaceae species forming a dense mat that is efficient in controlling soil erosion but in which other species hardly develop. Together, these data have clear consequences for revegetation of disturbed soils of graded ski slopes: optimization of the seeding practices (choice of the period to avoid frosts, addition of adapted 'nurse' species to the local mixtures, selection of suitable fertilizers or adjuvants) could help improve their success.

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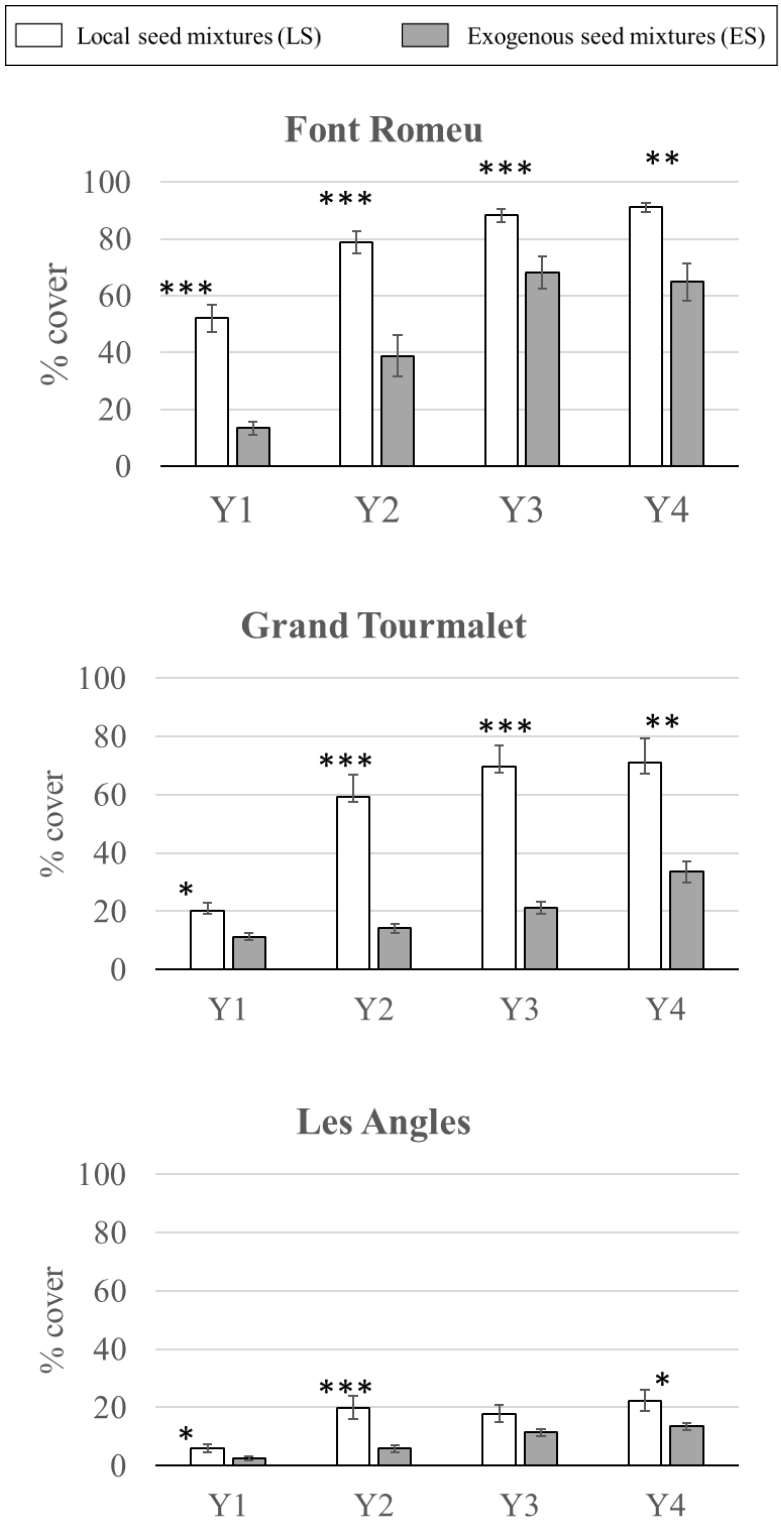
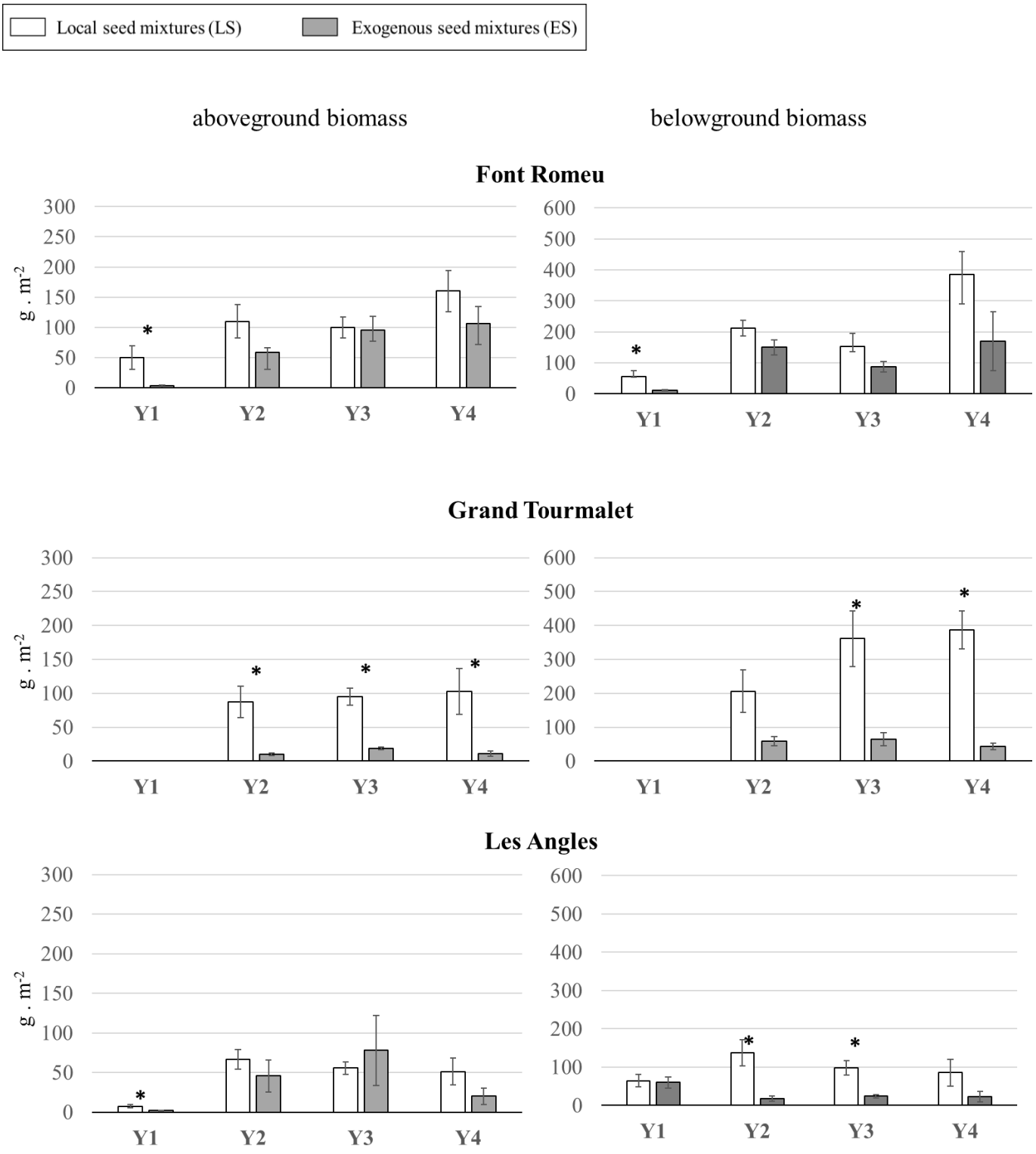
Figure 1- Dynamics of plant and soil parameters with local (white) and exogeneous (grey) seed mixtures at the three reclamation sites 1, 2, 3 and 4 years after seeding.). * (for $p = 0.05$), ** (for $p < 0.01$), and *** (for $p < 0.001$) "*" refer to statistically significant differences between local (LS) and exogenous (ES) seed mixtures at a given date (Mann-Withney test).

1a) total plant cover (expressed as % of quadrat surface)



1b) Plant aboveground and belowground biomasses



1c) Soil microbial activity (SIR rate)

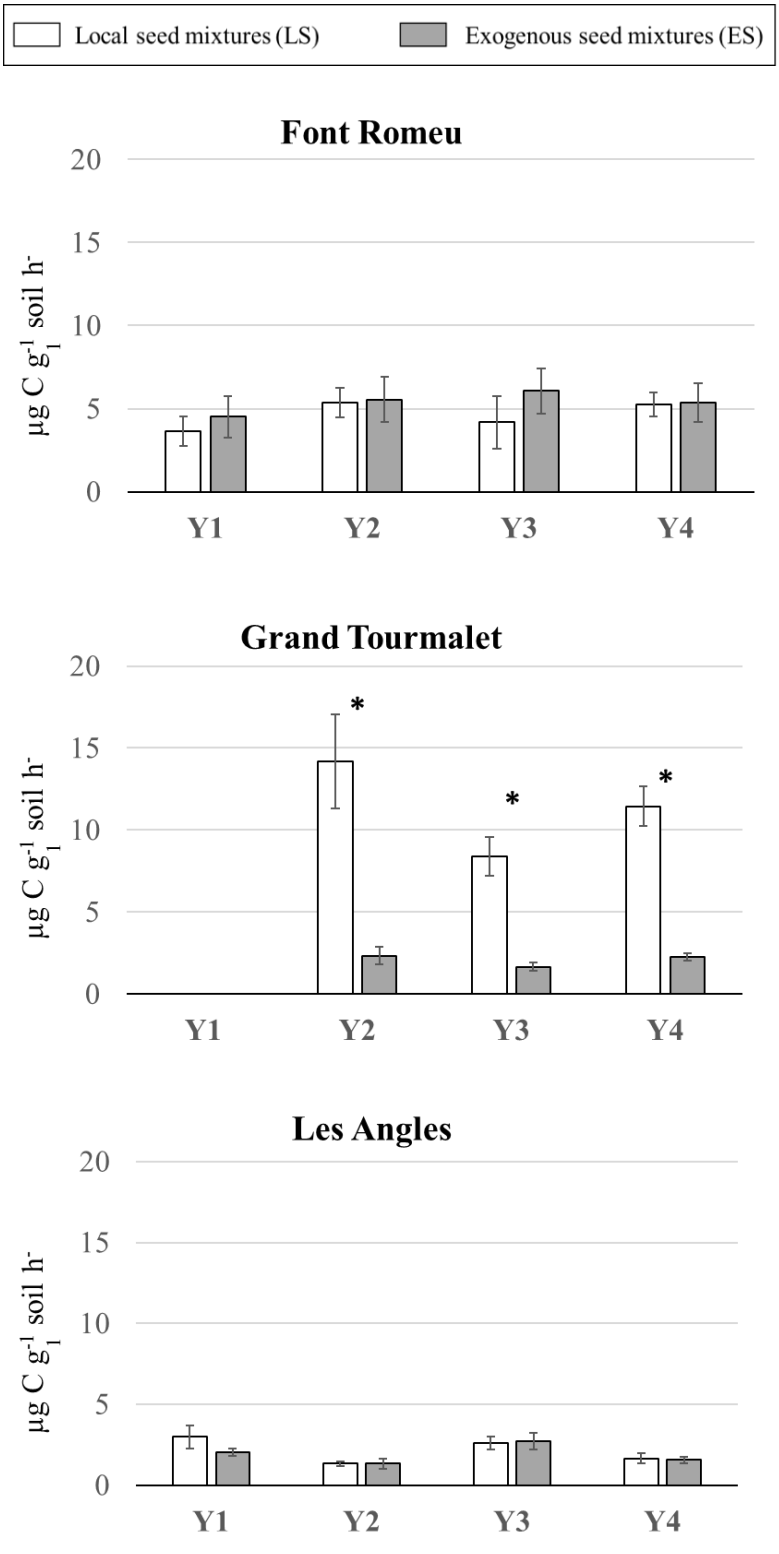


Figure 2- Nonmetric multidimensional scaling (NMDS) ordination of the plant community composition at the three sites Font Romeu (FR, circle labels), Grand-Tourmalet (GT, triangle labels) and Les Angles (LA, square labels) in the seed mixtures (in red) and in the plant cover after 1, 2, 3 and 4 years (Y1, Y2, Y3, Y4) in the plots that received local (white labels) or exogenous (grey labels) seed mixtures. The composition of the initial seed mixtures is plotted in red.

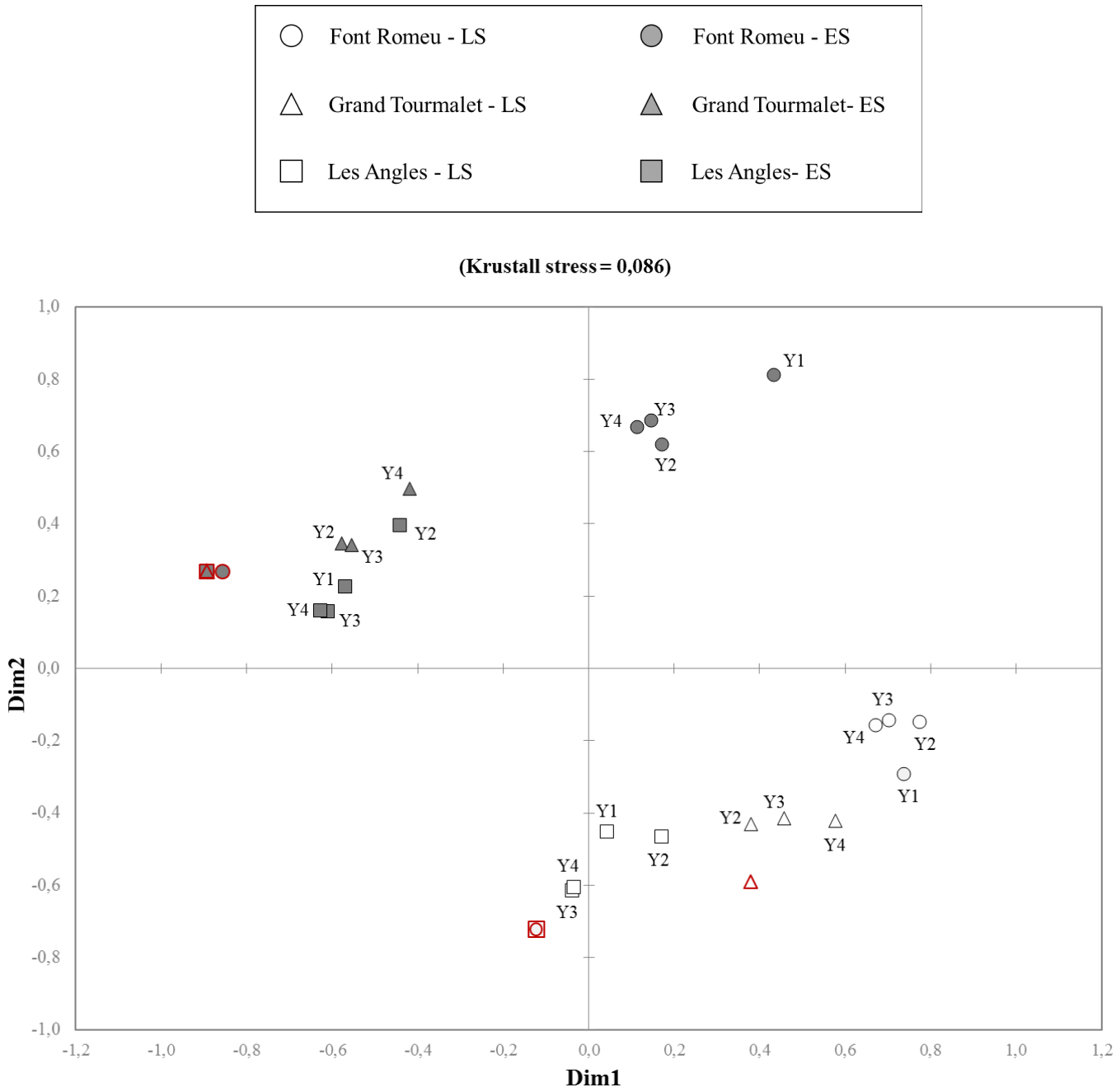
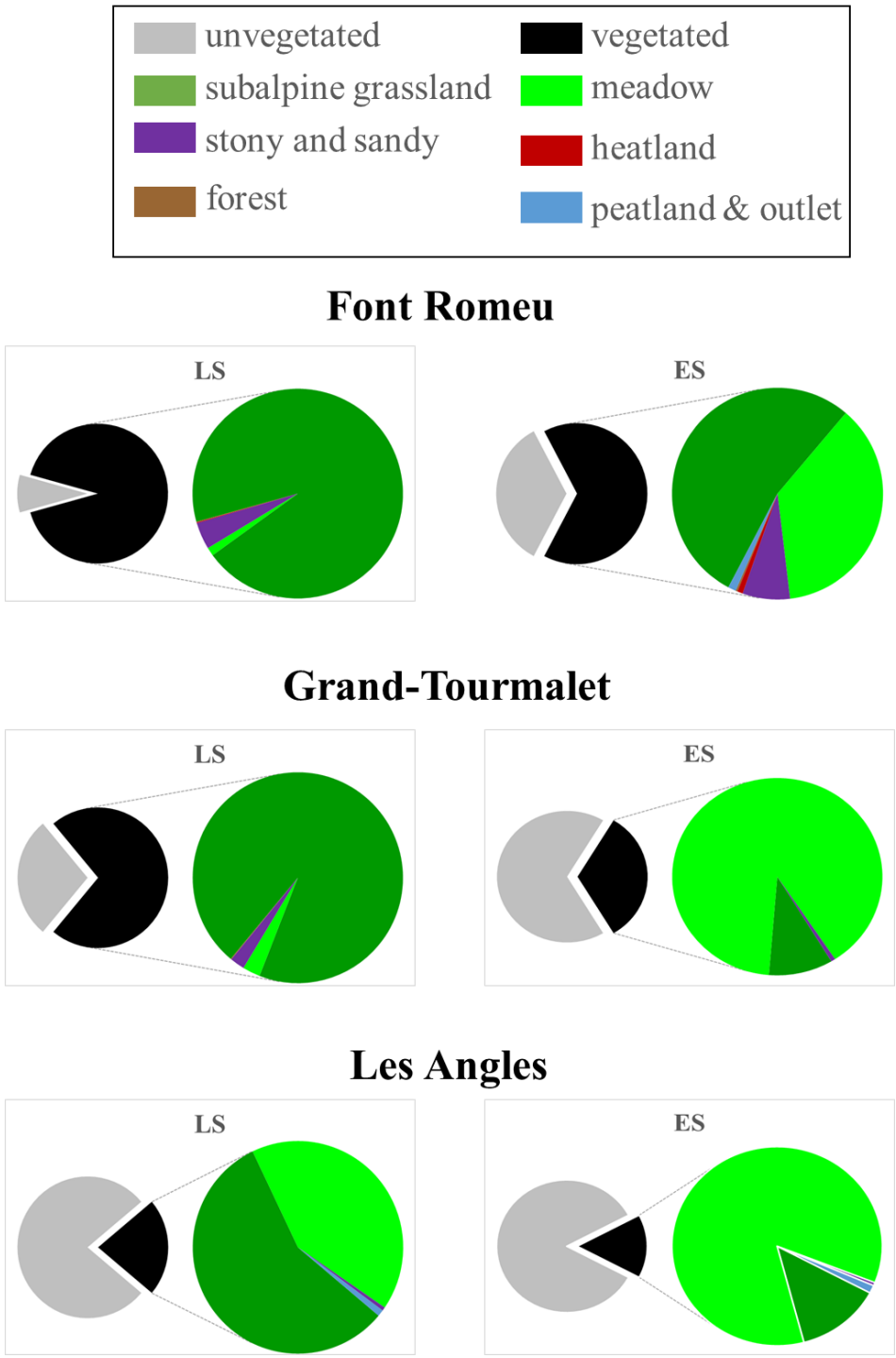


Figure 3- Vegetation at the three reclamation slope sites four years after seeding with local (LS) or exogeneous (ES) seed mixtures.

3a) Composition of the plant covers by habitat types (average percent cover across the 10 quadrats)



3b) Composition of the plant covers in terms of fodder value (fodder *vs* non-fodder species), and in -terms of seeded *vs* unseeded species.

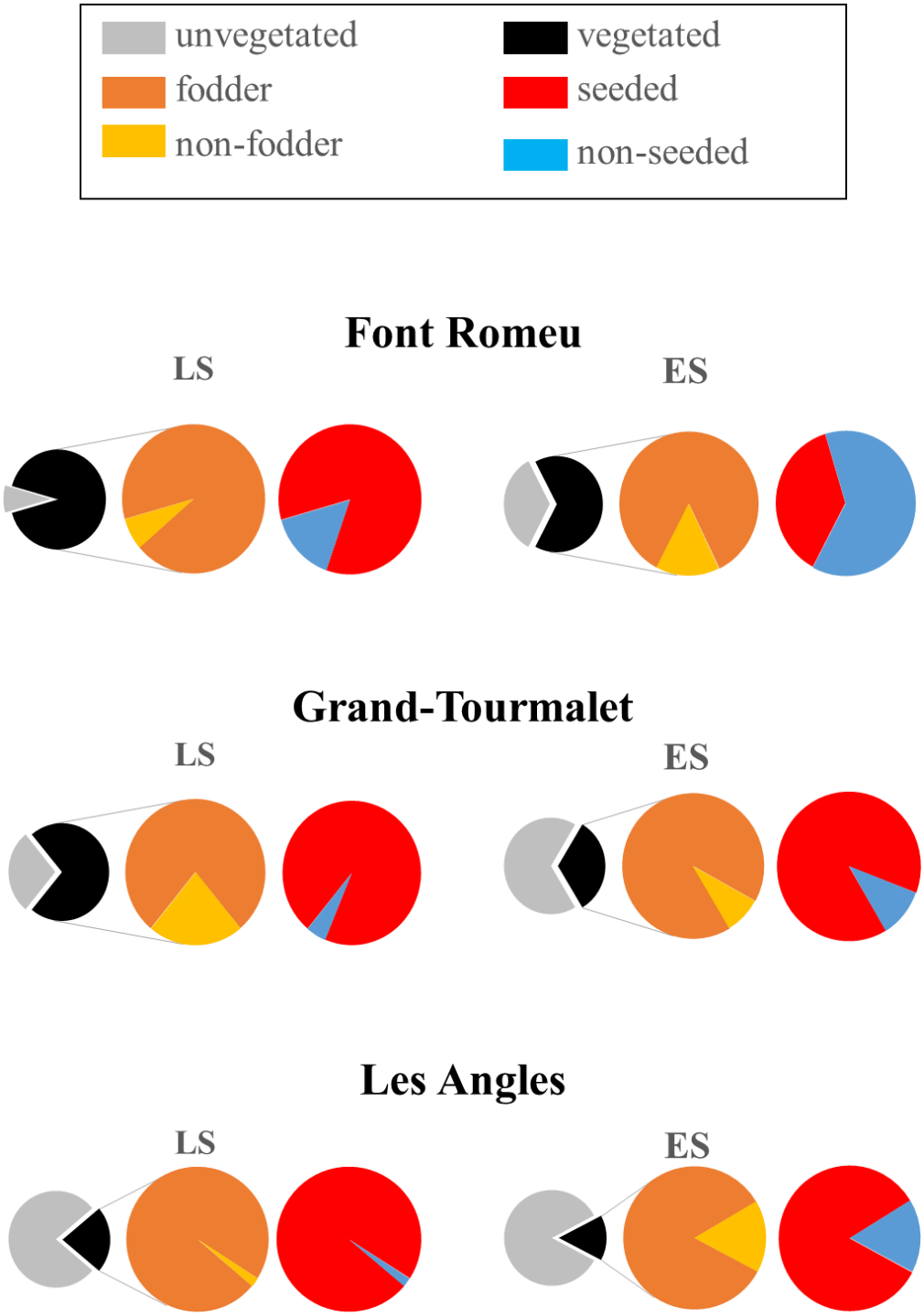


Table 1- Study sites, their characteristics and experimental assays.

Site	**Font Romeu**	**Grand Tourmalet**	**Les Angles**
Location	Pyrénées Orientales X : 620365,80 Y : 6159748,69	Hautes Pyrénées X : 466819,37 Y : 6205933, 58	Pyrénées Orientales X : 623105,89 Y : 6164375,53
Partner	Altiservice	SEMAP Peyragudes	RASL Les Angles
Seeding date	Oct. 2015	Oct. 2014	Nov. 2015
Substrate after grading	thick layer of topsoil (10 cm)	thin layer of topsoil (3 cm)	coarse sandy soil
Climate[a]: station (elevation) MAT / MAP	Font Romeu (1598 m) 6.2°C / 1072 mm	Barèges (1300 m) 4.6°C / 1776 mm	Les Angles (1677 m) 5.6°C / 1072 mm
Topography elevation slope exposition	2000 m a.s.l. 20 % North/East	2150 m a.s.l. 22% Sud	2000 m a.s.l. 30% East
Soil parameters[b] pH texture (clay/silt/sand, g kg^{-1}) gravel (% mass DW) soil C content (mg g^{-1}) soil N content (mg g^{-1}) soil P content (µg g^{-1}) CEC (cmol+ kg^{-1})	 4.94 121/186/693 43% 47.6 3.20 7.21 12.8	 4.91 250/369/381 45% 72.8 5.79 2.10 16.6	 5.90 41/139/821 52% 4.21 0.312 2.50 6.01
Surrounding vegetation	*Pinus uncinate* forest (less than 100 m away: *Nardion strictae*)	subalpine grassland (*Nardion strictae*)	*Pinus uncinate* forest (less than 100 m away: *Nardion strictae*)
Exogeneous seed assay commercial seed mixture sowing density plot size fertilizer[c] vegetal colloids hydromulch	**Font Rome ES** Pyrénées versant sud 250 kg ha^{-1} 1000 m² organo-mineral [5] (1000 kg ha^{-1}) 5 kg ha^{-1} 0 kg ha^{-1}	**Grand Tourmalet ES** Pyrénées versant sud 200 kg ha^{-1} 240 m² organo-mineral [5] (1040 kg ha^{-1}) 30 kg ha^{-1} 115 kg ha^{-1}	**Les Angles ES** Pyrénées Sud 250 kg ha^{-1} 922 m² organo-mineral [5] (1356 kg ha^{-1}) 33 kg ha^{-1} 1140 kg ha^{-1}
Local seed mixture origin	**Font Romeu LS** former hay meadow	**Grand Tourmalet LS** subalpine grassland	**Les Angles LS** former hay meadow

EUNIS code[d]	E.2.3	E.4.3	E.2.3
sowing density	260 kg ha^{-1}	100-150 kg ha^{-1}	200 kg ha^{-1}
plot size	260 m²	240 m²	350 m²
fertilizer[c]	organo-mineral (664 kg ha^{-1})	organic (1040 kg ha^{-1})	organo-mineral (3571 kg ha^{-1})
vegetal colloids	41 kg ha^{-1}	33 kg ha^{-1}	86 kg ha^{-1}
hydromulch	0 kg ha^{-1}	115 kg ha^{-1}	450 kg ha^{-1}

[a] CC climate.data.org (MAT: mean annual temperature and MAP: mean annual precipitation, period 1999-2019). Please note that the weather stations are located at lower elevation compared to assay sites.

[b] soil parameters were determined on a mix of five 0-10 cm depth topsoil samples at Y1 (average values for LS and ES plots), except for GT for which Y2 LS sample only could be analyzed; the corresponding data has therefore to be considered with caution.

[c] Organo-mineral fertilizer Amendine® 6-5-5 SK (SCPA du Roure) 6% N (3% organic N, 1% ammoniacal N, and 17% urea N), 5% P_2O_5, 5% K_2O, and 3% SO_3

[d] European Nature Information System https://eunis.eea.europa.eu/

Table 2- Number of species present in the seed mixtures and recorded in the plots (mean values ± standard error across the 4 (Font Romeu, Les Angles) or 3 (Grand-Tourmalet) sampling years. Detailed data (at each date) are shown in Supplementary Table S5.

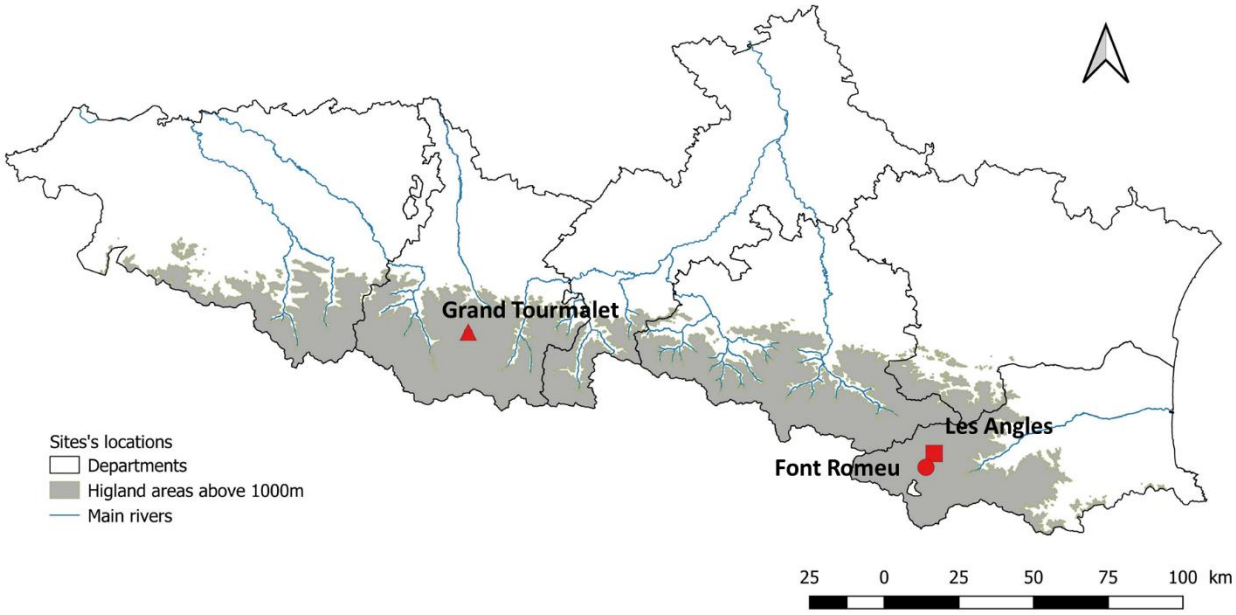
	Font Romeu LS	Grand Tourmalet LS	Les Angles LS	Font Romeu ES	Grand Tourmalet ES	Les Angles ES
in seed mixture	26	26	15	10	10	10
total	25.2 ± 0.8	19.3 ± 0.3	13.5 ± 0.9	26.8 ± 3.0	16.0 ± 0.6	13.3 ± 0.5
species in seed mix	6.8 ± 0.8	7.7 ± 0.3	6.0 ± 0.0	5.8 ± 0.5	8.0 ± 0.0	5.8 ± 0.3
‘target’ species	21 ± 0.9	17.0 ± 0.0	6.3 ± 0.8	18.5 ± 2.4	8 ± 0.6	4.8 ± 0.5
spontaneous species	18.5 ± 0.9	11.7 ± 0.3	7.5 ± 0.9	21 ± 3.2	8 ± 0.6	7.5 ± 0.5

Table 3- Number of species present in the seed mixtures and recorded in the plots (mean values ± standard error across the 4 (Font Romeu, Les Angles) or 3 (Grand-Tourmalet) sampling years. Detailed data (at each date) are shown in **Supplementary Table S5**.

	FR-LS	GT-LS	LA-LS	FR-ES	GT-ES	LA-ES
in seed mixture	26	26	15	10	10	10
total	25.2 ± 0.8	19.3 ± 0.3	13.5 ± 0.9	26.8 ± 3.0	16.0 ± 0.6	13.3 ± 0.5
species in seed mix	6.8 ± 0.8	7.7 ± 0.3	6.0 ± 0.0	5.8 ± 0.5	8.0 ± 0.0	5.8 ± 0.3
‘target’ species	21 ± 0.9	17.0 ± 0.0	6.3 ± 0.8	18.5 ± 2.4	8 ± 0.6	4.8 ± 0.5
spontaneous species	18.5 ± 0.9	11.7 ± 0.3	7.5 ± 0.9	21 ± 3.2	8 ± 0.6	7.5 ± 0.5

Supplementary material

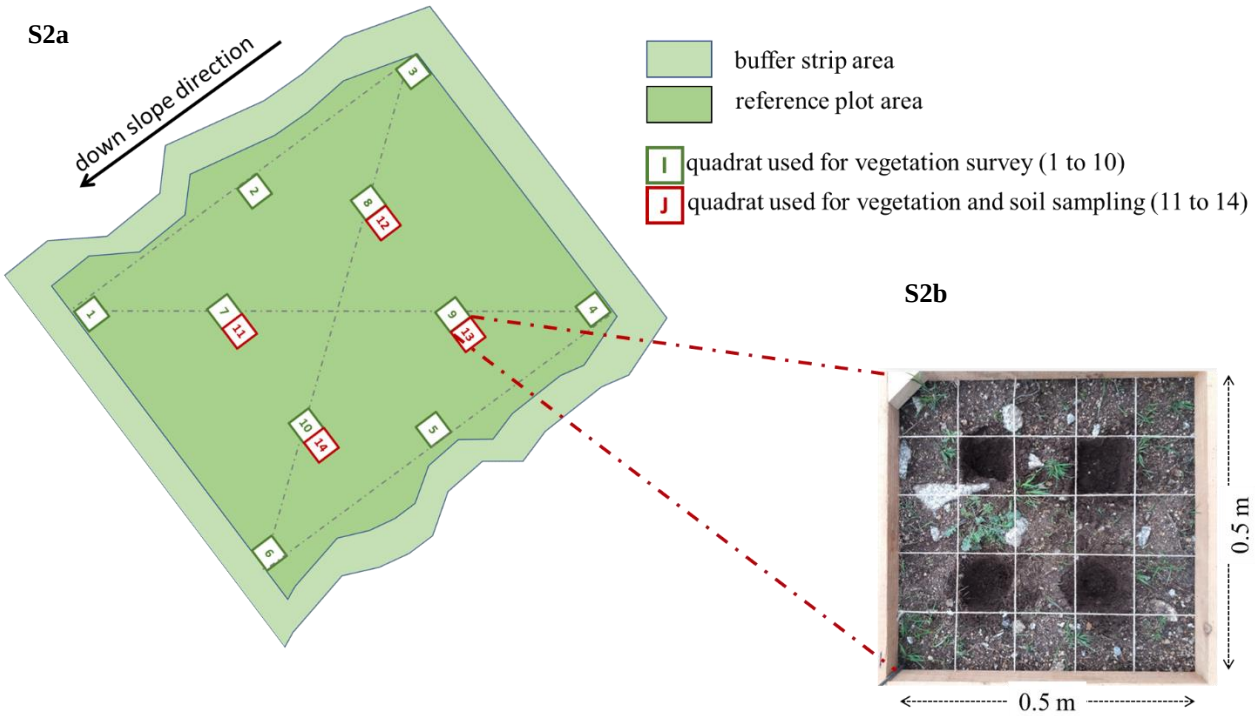
Supplementary material S1- Location of the sites



Supplementary material S2 – Sampling strategy

S2a: Distribution of quadrats across the studied plots (quadrats 1 to 10 for vegetation survey, quadrats 11 to 14 for plant biomass and soil sampling).

S2b: Sampling vegetation biomasses and soil in quadrats 11 to 14.



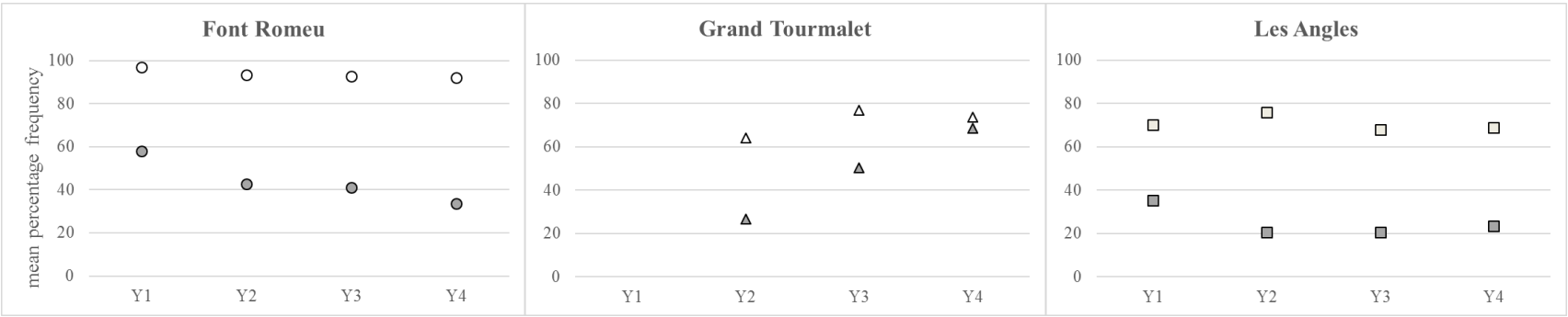
Supplementary material S3 –Poaceae percentage frequencies in plots seeded with local or exogenous seed mixtures at Font Romeu, Grand Tourmalet and Les Angles.

S3a- Percentage frequencies for Poaceae species (mean ± standard deviation, n = 10): For each quadrat, we recorded the species percentage frequency, as the number of squares in which the species is found divided by the total number of squares (i.e. 25). Species names **in bold** correspond to target species (from subalpine grasslands and stony/sandy habitats).

		Local seed mixture											Exogenous seed mixture										
		Font-Romeu				Grand-Tourmalet			Les Angles				Font Romeu				Grand-Tourmalet			Les Angles			
Species	sp	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4
Agrostis capillaris	**Ac**	**23,2% ±3,6%**	**17,6% ± 4,5%**	**40,4% ±5,6%**	**43,6% ±7,8**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**1,2% ± 0,7%**	**0,0%**	**0,0%**	**65,2% ± 8,4%**	**52,4% ± 32,5%**	**48,0% ± 29,9%**	**40,4% ± 33,3%**	**0,0%**	**0,0%**	**0,0%**	**0,4% ± 0,3%**	**0,8% ± 0,6%**	**0,8% ± 0,6%**	**0,0%**
Briza media L.	**Bm**	**2,8% ± 0,9%**	**0,0%**	**0,0%**	**0,0%**	**2,4% ± 1,1%**	**2,4% ± 1,3%**	**2,4% ± 1,9%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**
Dactylis glomerata	Dg	6,0% ± 2,3%	1,6% ± 1,0%	0,4% ± 0,3%	0,4% ± 0,3%	0,0%	0,0%	0,0%	2,0% ± 1,1%	3,2% ± 1,7%	4,8% ± 1,5%	6,4% ± 1,6%	16,0% ± 2,2%	10,0% ± 8,1%	11,6% ± 13,7%	8,0% ± 11,8%	26,0% ± 3,7%	32,2% ± 5,0%	6,4% ± 1,4%	8,4% ± 1,7%	5,6% ± 1,8%	28,0% ± 4,5%	33,2% ± 4,6%
Festuca eskia	**Fe**	**0,0%**	**0,0%**	**4,0% ± 2,2%**	**5,2% ± 2,8%**	**9,9% ± 1,6%**	**6,0% ± 2,1%**	**6,8% ± 2,4%**	**14,0% ± 1,8%**	**6,4% ± 1,4%**	**0,8% ± 0,8%**	**0,8% ± 0,2%**	**0,0%**	**6,8% ± 7,3%**	**6,0% ± 6,6%**	**4,0% ± 6,8%**	**2,0% ± 1,1%**	**5,2% ± 2,8%**	**11,6% ± 6,6%**	**0,4% ± 0,3%**	**0,8% ± 0,6%**	**7,6% ± 3,0%**	**11,2% ± 4,0%**
Festuca nigrescens	**Fn**	**100,0% ± 0%**	**100,0% ± 0%**	**100,0% ± 0%**	**100,0% ± 0%**	**69,6% ± 7,6%**	**89,6% ± 5,1%**	**89,2% ± 5,7%**	**86,0% ± 7,2%**	**83,6% ± 4,6%**	**72,0% ± 4,9%**	**73,2% ± 18,3%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**
Festuca rubra	Fr	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	20,8% ± 15,9%	36,0% ± 19,0%	30,0% ± 22,3%	47,2% ± 5,0%	76,4% ± 5,7%	81,6% ± 7,7%	60,4% ± 8,0%	10,8% ± 4,3%	25,6% ± 4,9%	30,4% ± 5,4%
Koeleria pyramidata	**Kp**	**1,2% ± 0,7%**	**0,8% ± 0,6%**	**0,4% 0,3%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**
Lolium perenne	Lp	2,8% ± 1,3%	3,6% ± 0,9%	0,0%	0,0%	0,0%	0,0%	0,0%	5,6% ± 1,0%	4,8% ± 1,2%	6,8% ± 2,6%	6,4% ± 1,6%	1,6% ± 0,8	4,0% ± 12,6%	0,0%	0,0%	0,0%	23,2% ± 3,4%	0,8% ± 0,6%	5,2% ± 1,1%	35,6% ± 8,3%	18,8% ± 4,1%	18,4% ± 4,3%
Nardus stricta	**Ns**	**3,6% ± 1,5%**	**4,4% ± 1,9%**	**4,8% ± 2,0%**	**7,2% ± 2,6%**	**8,4% ± 3,2%**	**12,0% ± 4,1%**	**34,0% ± 9,6%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,4% ± 1,3%**	**2,0% ± 3,4%**	**1,1% ± 1,9%**	**4,0% ± 1,2%**	**0,0%**	**6,4% ± 1,8%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**
Phleum pratense	Php	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,4% ± 0,3%	0,8% ± 0,6%	2,0% ± 1,1%	2,0% ± 1,1%
Poa alpina	**Poa**	**2,8% ± 0,8%**	**3,2% ± 0,9%**	**1,2% ± 0,9%**	**0,8% ± 0,4%**	**2,2% ± 1,0%**	**15,2% ± 3,6%**	**19,2% ± 5,0%**	**0,8% ± 0,4%**	**1,2% ± 0,9%**	**0,0%**	**0,0%**	**2,4% ± 1,9%**	**4,0% ± 7,1%**	**2,0% ± 6,3%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**	**0,0%**
Poa trivialis	Pop	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%
Schedonorus arundinaceus	Sca	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	0,0%	9,2% ± 2,8%	1,2% ± 3,8%	1,3% ± 0,4%	0,0%	0,0%	11,6% ± 2,6%	3,6% ± 2,8%	0,4% ± 0,3%	2,0% ± 0,8%	2,4% ± 1,1%	4,0% ± 1,7%

S3b- Mean percentage frequency for Poaceae in LS and ES plots at the three sites (Font Romeu, Grand Tourmalet, Les Angles)

The mean value was computed for all the Poaceae species present in the ten quadrat of a given plot, weighted by the relative contribution of the species to the total Poaceae cover. We did not compare the percentage frequencies for Poaceae species because different species occur in LS and ES plots (especially for *Festuca* spp.). The mean average frequencies are computed as: $\sum_i^j (percentage\ frequency(i) * \frac{\text{cover(i)}}{\sum_i^j cover\ (i)})$, with *cover(i)* is the relative cover for species i, and $\sum_i^j \text{cover(i)}$ is the total relative cover for all Poaceae species. Font Romeu (FR, circle labels), Grand-Tourmalet (GT, triangle labels) and Les Angles (LA, square labels) in the seed mixtures (in red) and in the plant cover after 1, 2, 3 and 4 years (Y1, Y2, Y3, Y4) in the plots that received local (white labels) or exogenous (grey labels) seed mixtures.



This graph shows that the mean percentage frequency for Poaceae is higher in the plots seeded with local (LS) compared to exogenous (ES) seed mixtures at the three experimental sites. At Font Romeu and Les Angles, Poaceae mean percentage frequency was at least two times higher in LS compared to ES plots, showing that Poaceae were better spread on the soil surface, while lower percentage frequencies in ES plots indicated that, in these plots, the plants grew in clusters and were less regularly spread. At Grand Tourmalet, the mean percentage frequency was higher in LS after 2 and 3 years as compared to that in ES plot, but such a difference disappeared after 4 years. As Poaceae species have extended roots system, they probably better contributed to the soil stabilization when more regularly spread.

Supplementary material S4- Estimation of plot covers following local (LS) and exogenous (ES) seed mixture seeding at Font Romeu, Grand Tourmalet and Les Angles ski slopes. Plant cover, FE: fine earth cover (%), CE<10: fine (< 10 mm) element cover (%), CE>10: coarse (> 10 mm) element cover (%), and others (moss, wood debris…). Cover values are averaged across ten quadrats per plot.

Results of mixed model testing for the effects of seed mixture and sampling date and their interactions on the relative covers of fine (<10 mm) and coarse (>10 mm) elements.

Fine elements (<10 mm) (%)

	seed mixture *F value*	date *F value*	Seed mixt. X date *F value*
Font Romeu	**15.28*** **	**20.62*** **	1.48
Grand-Tourmalet	**64.43*** **	**13.47*** **	**12.09*** **
Les Angles	0.035	**7.17*** **	0.97

Coarse elements (>10 mm) (%)

(%)	seed mixture *F value*	date *F value*	Seed mixt. x date *F value*
Font Romeu	**22.11*** **	1.18	0.87
Grand-Tourmalet	**221.76*** **	**26.90*** **	**17.79*** **
Les Angles	**40.69*** **	**3.95* **	2.32

Supplementary material S5- Species classification (by family ; habitat type, forage/non-forage species), their proportions in the seed mixtures and in the plant cover (relative percent cover), and species richness at the three experimental sites (Font Romeu, Grand Tourmalet, Les Angles) at the three or four sampling years (Y1 to Y4). Species in bold correspond to target species (from subalpine grasslands and stony/sandy habitats).

S5a: Species that present in at least one of the seed mixtures, that are successful (i.e. recorded in the corresponding plot covers, in red), unsuccessful (i.e. not recorded in the corresponding plot covers, in blue), or spontaneous (not present in the corresponding seed mixture, in green) and their relative cover in the LS and ES plots.

					LS plots											ES plots											seed mixtures			
					Font-Romeu				Grand-Tourmalet			Les Angles				Font Romeu				Grand-Tourmalet			Les Angles				Font Romeu / Les Angles LS	Grand Tourmalet LS	Font Romeu ES	Grand Tourmalet / Les Angles
Species present in seed mixtures	Family	Typical habitat	sp	Forage interest	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4				
Achillea millefolium L.	Asteraceae	Meadow	Am	Forage	0,91	0,37	0,66	0,93	9,03	8,50	2,72	5,83	5,56	9,98	7,74	2,25	6,18	8,52	6,53	3,57	4,18	2,62	4,28	2,71	18,93	19,56	6,20	3,00	1,00	1,00
Anthoxanthum odoratum L.	Poaceae	Meadow	Ao	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,10	0	0	0
Avenella flexuosa (L.) Drejer	Poaceae	Peatland & outlet	Af	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2,30	0	0
Bistorta officinalis Delarbre	Polygonaceae	Meadow	Bo	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,60	0	0	0
***Briza media* L.**	**Poaceae**	**Subalpine grassland**	**Bm**	**Forage**	**0,31**	**0**	**0**	**0**	**0,51**	**0,43**	**0,42**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1,51**	**1,20**	**0**	**0**
***Carex brizoides* L.**	**Cyperaceae**	**Stony and sandy habitat**	**Cb**	**Non forage**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1,20**	**0**	**0**	**0**
Carex nigra (L.) Reichard	Cyperaceae	Peatland & outlet	Can	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,20	0,30	0	0
***Conopodium majus* (Gouan) Loret**	**Apiaceae**	**Subalpine grassland**	**Cma**	**Non forage**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,20**	**0,18**	**0**	**0**
Dactylis glomerata L.	Poaceae	Meadow	Dg	Forage	0,31	0,51	0,05	0,11	0	0	0	1,11	0,79	1,29	1,80	6,74	3,90	3,54	2,59	10,22	11,59	2,07	21,39	21,08	25,00	18,02	1,60	0	15,00	15,00
***Dianthus deltoides* L.**	**Caryophyllaceae**	**Subalpine grassland**	**Dd**	**Non forage**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,01**	**0,70**	**0**	**0**
***Festuca eskia* Ramond ex DC.**	**Poaceae**	**Subalpine grassland**	**Fe**	**Non forage**	**0**	**0**	**1,37**	**1,36**	**3,25**	**3,75**	**4,44**	**8,06**	**1,77**	**0,21**	**0,18**	**0**	**3,24**	**1,53**	**4,12**	**4,12**	**3,80**	**6,10**	**2,67**	**6,02**	**8,05**	**12,23**	**0**	**4,10**	**0**	**0**
***Festuca nigrescens* L.**	**Poaceae**	**Subalpine grassland**	**Fn**	**Forage**	**90,91**	**84,60**	**84,89**	**82,46**	**74,92**	**72,50**	**69,96**	**60,28**	**66,81**	**53,65**	**56,26**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**60,73**	**79,10**	**0**	**0**
Festuca rubra L.	Poaceae	Meadow	Fr	Forage	0	0	0	0	0	0	0	0	0	0	0	0	5,16	26,87	27,63	50,75	51,66	77,74	41,71	12,95	18,93	24,97	0	0	30,00	25,00
***Galium verum* L.**	**Rubiaceae**	**Subalpine grassland**	**Gv**	**Non forage**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,30**	**0,20**	**0**	**0**
***Jasione laevis* L.**	**Campanulaceae**	**Subalpine grassland**	**Jl**	**Non forage**	**0**	**0**	**0**	**0**	**0,24**	**0,14**	**0,14**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,19**	**0,12**	**0**	**0**	**0**	**0**	**0**	**0,30**	**0**	**0**
***Koeleria pyramidata* (Lam.) P.Beauv.**	**Poaceae**	**Stony and sandy habitat**	**Kp**	**Forage**	**0,16**	**0,05**	**0,09**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**3,64**	**0**	**0**	**0**
Lolium perenne L.	Poaceae	Meadow	Lp	Forage	0,24	0,28	0	0	0	0	0	5,28	3,09	1,93	1,89	0,56	4,05	0	0	10,22	3,32	0,55	8,56	45,78	16,24	11,20	5,00	0	10,00	15,00
***Lotus corniculatus* L.**	**Fabaceae**	**Subalpine grassland**	**Loc**	**Forage**	**0,31**	**0,18**	**0,20**	**0,20**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1,26**	**0,76**	**0,67**	**0,73**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,02**	**1,00**	**0**
Medicago sativa L.	Fabaceae	Meadow	Ms	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,00	0
***Nardus stricta* L.**	**Poaceae**	**Subalpine grassland**	**Ns**	**Non forage**	**0,24**	**0,60**	**0,59**	**1,26**	**2,98**	**6,82**	**13,19**	**0**	**0**	**0**	**0**	**0**	**0,10**	**0,22**	**0,21**	**1,51**	**1,23**	**1,28**	**0**	**0**	**0**	**0**	**2,60**	**5,30**	**0**	**0**
Onobrychis viciifolia Scop.	Fabaceae	Meadow	Ov	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10,00	5,00
Phleum pratense L.	Poaceae	Meadow	Php	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12,21	12,73	5,49	1,07	0,60	0,99	1,54	0,80	0	0	13,00
Plantago lanceolata L.	Plantaginaceae	Meadow	Pll	Forage	0	0	0	0	0	0,14	0	0,56	5,03	2,25	1,44	0	0	0	0	0,27	0,38	0,12	0	0	0,28	0,26	0,10	0	0	1,00
***Plantago monosperma* Pourr.**	**Plantaginaceae**	**Stony and sandy habitat**	**Pmo**	**Forage**	**0,08**	**0,09**	**0,09**	**0,22**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,07**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,20**	**0**	**0**
***Poa alpina* L.**	**Poaceae**	**Subalpine grassland**	**Poa**	**Forage**	**1,14**	**1,57**	**0,05**	**0,22**	**0,58**	**2,90**	**4,41**	**1,11**	**0,62**	**0**	**0**	**1,40**	**0,61**	**0,07**	**0**	**0**	**0,19**	**0**	**0**	**0**	**0**	**0**	**0**	**1,20**	**0**	**0**
Poa trivialis L.	Poaceae	Meadow	Pot	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,05	0	0	0
***Poterium sanguisorba* L.**	**Rosaceae**	**Subalpine grassland**	**Ps**	**Forage**	**0,08**	**0,05**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,56**	**0,41**	**0**	**0,06**	**0**	**0**	**0**	**6,42**	**0**	**0**	**0**	**0,10**	**0**	**6,00**	**3,00**
Ranunculus acris L.	Ranunculaceae	Meadow	Raa	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,30	0	0	0
Rhinanthus minor L.	Orobanchaceae	Meadow	Rm	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,74	0	0	0
Schedonorus arundinaceus (Shreb.) Dumort.	Poaceae	Meadow	Sca	Forage	0	0	0	0	0	0	0	0	0	0	0	1,40	0,25	0,07	0	2,74	4,56	0,73	1,07	1,20	6,64	5,66	0	0	25,00	20,00
***Scorzoneroides pyrenaica* (Gouan) Holub**	**Asteraceae**	**Stony and sandy habitat**	**Spy**	**Non forage**	**0**	**0,46**	**0,20**	**0,20**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,84**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0,30**	**0**	**0**	**0**
Taraxacum sp. F.H.Wigg.	Asteraceae	Peatland & outlet	To	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,01	0	0	0
Tragopogon pratensis L.	Asteraceae	Meadow	Trp	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,01	0	0	0
Trifolium pratense L.	Fabaceae	Meadow	Tpr	Forage	0	0	0	0	0	0	0	0	0	0	0	0,84	0	0	0	0	0	0	0	0	0	0	0,30	0	0	0
Trifolium repens L.	Fabaceae	Meadow	Tr	Forage	0	0	0	0	1,71	0,28	0	4,44	13,68	28,43	28,80	0	0	0	0	0,27	0,38	0,12	6,95	0	2,12	2,57	10,30	1,90	1,00	2,00
Vicia sepium L.	Fabaceae	Peatland & outlet	Vs	Forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,10	0	0	0

S5b: Species that are spontaneous (*i.e.* not present in the seed mixtures but recovered in the plant covers, in green) and their relative cover in the LS and ES plots.

					LS plots											ES plots										
					Font-Romeu				Grand-Tourmalet			Les Angles				Font Romeu				Grand-Tourmalet			Les Angles			
Species present in seed mixtures	Family	Optimun natural habit	sp	Forage interest	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4
***Agrostis capillaris* L.**	**Poaceae**	**Subalpine grassland**	**Ac**	**Forage**	0,87	3,65	8,24	8,29	0,07	0,06	0,06	0	0,97	0	0	65,59	56,20	45,03	45,02	0	0	0	1,07	5,12	0,28	0
***Alchemilla alpina* L.**	**Rosaceae**	**Stony and sandy habitat**	**Aa**	**Non forage**	0	0	0	0	0	0	0	0	0	0	0	0	0	0,56	0,55	0	0	0	0	0	0	0
Anemone nemorosa L.	Ranunculaceae	Meadow	An	Non forage	0	0	0,05	0,06	0	0	0	0	0	0	0	0,56	0	0	0	0	0	0	0	0	0	0
***Atocion rupestre* (L.) B.Oxelman**	**Caryophyllaceae**	**Stony and sandy habitat**	**Ar**	**Non forage**	0,08	3,88	0,36	0	0,51	0,43	0,17	0,56	0,18	0,43	0,36	0	0,96	0,82	0,73	0	0	0	1,07	1,20	0,28	0,26
Calluna vulgaris L. Hull	Ericaceae	Heatland	Cv	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Carex caryophyllea* Latourr.**	**Cyperaceae**	**Subalpine grassland**	**Cc**	**Non forage**	0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,76	0	0	0	0	0	0	0
Cirsium eriophorum (L.) Scop.	Asteraceae	Peatland & outlet	Ce	Non forage	0	0	0	0	0	0	0	0	0	0,43	0,36	0	0	0	0	0	0	0	0	0	0,99	1,29
***Coincya monensis subsp. cheiranthos* (Vill.)**	**Brassicaceae**	**Stony and sandy habitat**	**Cmo**	**Non forage**	0,24	0,09	0,09	0,13	0	0	0	0	0	0	0	0	0,20	0,07	0,06	0	0	0	0	0	0	0
***Crocus nudiflorus* Sm.**	**Iridaceae**	**Subalpine grassland**	**Crn**	**Non forage**	0,16	0,05	0	0	0,58	0,06	1,22	0	0	0	0	0,56	0	0,07	0	0,55	0	0	0	0	0	0
Cytisus oromediterraneus Rivas Mart. & al.	Fabaceae	Heatland	Co	Non forage	0,39	0,09	0,14	0,18	0	0	0	0	0	0	0	1,40	0,81	0,30	0,24	0	0	0	0	0	0	0
***Galium pumilum* Murray**	**Rubiaceae**	**Subalpine grassland**	**Gap**	**Non forage**	0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,15	0	0	0	0	0	0	0
***Galium saxatile* L.**	**Rubiaceae**	**Subalpine grassland**	**Gas**	**Non forage**	0	0	0	0	0,68	1,28	0,56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Gnaphalium sylvaticum* L.**	**Asteraceae**	**Subalpine grassland**	**Gns**	**Non forage**	0	0	0	0	0	0	0,14	0	0	0	0	0	0	0	0	0,27	0,95	0,12	0	0	0	0
Hypochaeris radicata L.	Asteraceae	Meadow	Ha	Non forage	0	0	0	0	0	0	0	1,67	0,18	0	0	0	0	0	0	0	0	0	0	0	0,71	1,29
Leontodon hispidus L.	Asteraceae	Meadow	Lh	Non forage	0	0	0	0	0	0	0	0	0,18	0	0	0	0	0	0	0	0	0	0	0	0	0
Leucanthemum vulgare Lam.	Asteraceae	Meadow	Lv	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,15	0	0	0	0	0	0	0
***Linaria repens* (L.) Mill.**	**Plantaginaceae**	**Stony and sandy habitat**	**Lr**	**Non forage**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,26
***Luzula campestris* (L.) DC.**	**Juncaceae**	**Subalpine grassland**	**Luc**	**Non forage**	0	0	0	0	0	0	0	0	0	0	0	0	0	0,60	0,49	0	0	0	0	0	0	0
***Meum athamanticum* Jacq.**	**Apiaceae**	**Subalpine grassland**	**Ma**	**Non forage**	0,94	0,16	0,23	0,33	0	0	0	0	0	0	0	0,28	1,27	1,38	1,07	0	0	0	0	0	0	0
***Murbeckiella pinnatifida* (Lam.)**	**Brassicaceae**	**Stony and sandy habitat**	**Mp**	**Non forage**	0,08	0,05	0,11	0,15	0,31	0,14	0,06	0	0,35	0,21	0,18	0	0,35	0,15	0	1,37	0	0	0	0	0	0
***Paronychia polygonifolia* (Vill.) DC.**	**Caryophyllaceae**	**Stony and sandy habitat**	**Pap**	**Non forage**	0,16	0,67	0,32	0,42	0,82	0,57	0,53	0	0	0	0	1,26	1,42	1,60	1,71	0	0	0,12	0	0	0	0
Pinus mugo subsp. *uncinata* (Ramond ex DC.) Domin	Pinaceae	Forest	Pim	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,15	0	0	0	0	0	0	0
***Plantago maritima* L.**	**Plantaginaceae**	**Subalpine grassland**	**Pma**	**Forage**	0,31	0,14	0,05	0,04	0	0	0	0	0	0	0	0,98	4,71	2,08	2,11	0	0	0	0	0	0	0
***Pilosella lactucella* (Wallr.) P.D.Sell & C.West**	**Asteraceae**	**Subalpine grassland**	**Pil**	**Non forage**	0	0	0,05	0,04	0	0	0	1,67	0	0	0	0	0	0,15	0,21	0	0	0	1,07	0,60	0	0
***Pulsatilla alpina* (L.) Delarbre**	**Ranunculaceae**	**Subalpine grassland**	**Pua**	**Non forage**	0	0,05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Ranunculus pyrenaeus* subsp. *pyrenaeus* L.**	**Ranunculaceae**	**Subalpine grassland**	**Rp**	**Non forage**	0	0	0	0	0,34	0,14	0,06	0	0	0	0	0	0	0	0	0	0	0,12	0	0	0	0
Rumex acetosa L.	Polygonaceae	Meadow	Rat	Non forage	0	0	0	0	0	0	0	1,94	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Rumex acetosella* L.**	**Polygonaceae**	**Stony and sandy habitat**	**Ral**	**Non forage**	0,16	0,79	0,23	0,40	0	0	0	0	0	0,43	0,36	0	0,20	0,22	0,27	0	0	0	2,67	1,51	0,56	0,90
***Sagina saginoides* subsp. *pyrenaica* (Rouy) Font Quer**	**Caryophyllaceae**	**Subalpine grassland**	**Ss**	**Non forage**	0	0	0	0	0,07	0,14	0	0	0	0	0	0	0	0	0	0,27	0	0	0	0	0	0
***Scleranthus perennis* L.**	**Caryophyllaceae**	**Stony and sandy habitat**	**Spe**	**Non forage**	0,67	0,09	0,09	0,15	0	0	0	0	0	0	0	0	2,03	0,37	0,61	0	0	0	0	0	0	0
***Sesamoides pygmaea* (Scheele) Kuntze**	**Resedaceae**	**Stony and sandy habitat**	**Sep**	**Non forage**	0	0,18	1,50	2,28	0	0	0	4,17	0	0	0	0	1,52	1,27	1,04	0	0	0	0	0	0	0
Sisymbrium austriacum Jacq.	Brassicaceae	Peatland & outlet	Sia	Non forage	0	0	0	0	0	0	0	0	0,18	0,75	0,63	0	0	0	0	0	0	0	0	1,20	0	0
***Spergularia rubra* (L.) D. Dietr.**	**Caryophyllaceae**	**Stony and sandy habitat**	**Sr**	**Non forage**	1,06	0,62	0,27	0,40	2,63	1,14	0,11	1,11	0,62	0	0	7,30	1,42	0,45	0,46	0	0,38	0,43	0	0	0	0
***Trifolium alpinum* L.**	**Fabaceae**	**Subalpine grassland**	**Ta**	**Forage**	0	0,05	0,05	0,11	0,68	0,43	0,33	0	0	0	0	5,90	1,52	0,19	0,37	1,37	4,46	2,13	0	0	0	0
Vaccinium myrtillus L.	Ericaceae	Peatland & outlet	Vm	Non forage	0	0	0	0	0	0	0	0	0	0	0	0	1,57	1,56	0,61	0	0	0	0	0	0	0
***Veronica arvensis* L.**	**Plantaginaceae**	**Stony and sandy habitat**	**Va**	**Non forage**	0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
***Veronica fruticans* Jacq.**	**Plantaginaceae**	**Stony and sandy habitat**	**Vf**	**Non forage**	0,20	0,67	0,05	0,04	0,07	0,14	1,39	0	0	0	0	0,28	0,41	1,12	1,22	0,27	0	0,12	0	0	0	0
Viola recheinbachiana Jord. ex Boreau	Violaceae	Forest	Vr	Non forage	0	0	0	0	0	0	0,11	0	0	0	0	0	0,76	0,15	0,12	0	0	0	0	0	0	0

S5c: Number of species recorded in the plots: total species richness, number of target species (*i.e.* from subalpine grassland or sandy/stony habitat), spontaneous (*i.e.* not present in the corresponding seed mixture) and seeded species in the LS and ES plots.

	LS plots											ES plots										
	Font-Romeu				Grand Tourmalet			Les Angles				Font Romeu				Grand Tourmalet			Les Angles			
	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4
total number of species (richness)	**24**	**27**	**26**	**24**	**19**	**20**	**19**	**15**	**15**	**12**	**12**	**19**	**26**	**33**	**29**	**16**	**15**	**17**	**13**	**12**	**14**	**14**
number of target species	**20**	**23**	**22**	**19**	**17**	**17**	**17**	**8**	**7**	**5**	**5**	**12**	**18**	**23**	**21**	**8**	**7**	**9**	**6**	**5**	**4**	**4**
numbre of spontaneous target species	**15**	**18**	**18**	**16**	**11**	**11**	**11**	**7**	**6**	**4**	**4**	**10**	**16**	**22**	**19**	**8**	**7**	**9**	**5**	**5**	**4**	**4**
number of spontaneous species	**16**	**19**	**20**	**19**	**11**	**12**	**12**	**9**	**9**	**6**	**6**	**13**	**19**	**28**	**24**	**8**	**7**	**9**	**8**	**6**	**8**	**8**
number of seeded species	**8**	**8**	**6**	**5**	**8**	**8**	**7**	**6**	**6**	**6**	**6**	**6**	**7**	**5**	**5**	**8**	**8**	**8**	**5**	**6**	**6**	**6**

Supplementary material S6- Some pictures of the experimental plots showing soil erosion following the use of exogenous seed mixtures

a) Gullies formed on the ES plot at Font Romeu, three years after seeding with exogenous seed mixture (2018)

b) Gullies formed at Grand-Tourmalet site one year after seeding with exogenous mixture.

c) Gullies forming at Les Angles, one year after seeding with exogenous seed mixture (2016)