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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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25

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33

34 Keywords: native seeds, exogeneous seeds, reclamation, prairie restoration, subalpine
35 grassland, soil microbial activity

36

37

38 **Highlights**

39 • Seeds harvested close to ski slopes can be useful for the restoration of plant cover.

40 • Local seed mixtures were more efficient than exogenous ones to restore plant
41 cover on the ski slopes.

42 • The efficiency of revegetation was highly dependent on local soil conditions.

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45

46 **Abstract**

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

61

62

63 **1. Introduction**

64

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

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

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

91 Current erosion-control practices on ski slopes include seeding with commercial
92 mixtures generally dominated by non-native grass and legume species (Burt & Rice 2009),
93 largely recommended by seed companies. However, these mixtures do not always establish
94 successfully even despite high fertilizer inputs (Tsuyuzaki 1995; Krautzer et al. 2006, Burt
95 2012, Swab et al. 2017), resulting in a poor control of soil erosion. Furthermore, non-native
96 species can generate unintended effects such as the establishment of ruderal woody species
97 (ski slopes are frequently located in forest, with the nearby vegetation including woody
98 species that are undesirable on the slopes), and resistance to the establishment of native, local
99 plant species (Tsuyuzaki 1995; Burt & Rice, 2009; Burt 2012; Barrantes et al., 2013; Hagen
100 et al. 2014), although Hudek et al. (2020) found an increased colonization of native plant
101 species on a ski run in the Italian Alps 17 years after seeding with commercial seed mixtures.
102 Finally, the introduction of exogeneous plant material may lead to genetic evolution of the
103 wild adjacent plants due to hybridization process (Gauthier, 1997).

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

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

129 The existing literature reports few data about the impact seed material on the plant
130 roots (but see Hudek et al. 2020) nor on the soil microbial community (but see Swab et al.
131 2017). Yet, plant diversity and soil microbial community are tightly coupled, both explaining
132 ecosystem processes such as soil fertility or stability. For instance, in their study on mountain
133 grasslands, Grigulis et al. (2013) showed an equal contribution of plant and microbial
134 functional parameters in explaining soil organic matter content. Plant and soil microbial
135 parameters both control soil stability (Pérès et al. 2013; Blankinship et al. 2016), with roots
136 stabilizing the soil by mechanical effect, and the finer roots together with soil

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

149

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

158

159

160 2- Material and Methods

161

162 2.1- Study sites and assays

163

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

174

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

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

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

185 The exogeneous commercial seed mixture at Grand Tourmalet and Les Angles (mixture
186 Pyrénées Sud, company Gazon de France, France) was: *Schedonorus arundinaceus* (20%),
187 *Festuca rubra* (25%), *Dactylis glomerata* (15%), *Lolium perenne* (15%), *Onobrychis*
188 *viciifolia* (5%), *Poterium sanguisorba* (3%), *Phleum pratense* (13%), *Plantago lanceolata*
189 (1%) *Trifolium repens* var *Huia* (2%) *Achillea millefolium* (1%).

190 Local seeds at Font Romeu and Les Angles were yielded from former hay meadow (elevation
191 1690 m), with *Festuca nigrescens* (60.73% final mass), *Nardus stricta* (2.60%), *Koeleria*
192 *pyramidata* (3.64%), *Briza media* (1.51%) *Ranunculus acris* (1.30%), *Carex brizoides*
193 (1.20%), *Anthoxanthum odoratum* (1.10%), *Rhinanthus minor* (0.74%), *Bistorta officinalis*
194 (0.60%), *Galium verum* (0.30%), *Scorzoneroideis pyreanica* (0.30%), *Trifolium pratense*
195 (0.30%), *Carex nigra* (0.20%), *Conopodium majus* (0.20%), *Plantago lanceolata* (0.10%),
196 *Vicia sepium* (0.10%), *Dianthus deltoides* (0.01%), *Taraxacum sp.* (0.01%), *Tragopogon*
197 *pratensis* (0.01%), *Achillea millefolium* (6.20%), *Dactylis glomerata* (1.60%), *Poa trivialis*
198 (1.05%), *Phleum pratense* (0.80%), *Poterium sanguisorba* (0.10%). *Trifolium repens*
199 (10.30%) and *Lolium perenne* (5.0%) from exogenous origin were added as ‘nurse’ species
200 to this mixture.

201 Local seeds at Grand Tourmalet came from a nearby subalpine grassland (*Nardion strictae*,
202 elevation 1930 m) with *Festuca nigrescens* (79.10%), *Nardus stricta* (5.30%), *Festuca eskia*
203 (4.10%), *Briza media* (1.20%), *Avenella flexuosa* (2.30%), *Poa alpina* (1.20%), *Dianthus*
204 *deltoides* (0.70%), *Carex nigra* (0.3%), *Galium verum* (0.20%), *Conopodium majus* (0.18%),
205 *Jasione laevis* (0.30%) , *Plantago monosperma* (0.20%), *Achillea millefolium* (3.00%), *Lotus*

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

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

216

217 2.2- Vegetation survey

218

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

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

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

235

236 *2.3- Plant biomass and soil sampling*

237

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

250

251 *2.4- Soil microbial activity*

252

253 Substrate induced respiration (SIR) was determined as a proxy of the soil microbial biomass
254 and activity (Nannipieri et al. 2003) according to Beare et al. (1990). Briefly, 20 g air-dried
255 2-mm sieved soil samples were incubated in 150 mL sealed serum flasks at 80% field
256 capacity with 1.5 mg C-glucose g⁻¹ soil and at 25°C; two-hundred µL air samples from the
257 headspace were analysed after 2 and 6 hours for CO₂ concentration in the flasks using a
258 microcatharometer (MicroGC serie S, SRA Industries, Marcy l'Etoile, France) equipped with
259 a PoraPlot column (Agilent, Santa Clara, United States). SIR rates were calculated as the
260 mass of C-glucose converted to C-CO₂ per g of soil DW and per hour (µg C-CO₂ g⁻¹ soil h⁻¹).
261

262

263 2.5- Data analysis

264

265 Vegetation and microbial data were analysed with XL-STAT 2017 and R version 3.2.2.
266 Because the data were collected in unique, experimental plots per treatment at each ski slope
267 (site), the quadrats could not be used as true replicates. To deal with this issue, the effect of
268 local vs exogenous seed mixtures on vegetation percent covers was tested across the three
269 experimental sites and the four sampling dates using mixed models with repeated measures.
270 The site (ski slope) was used as random factor and the interaction between site and seed
271 mixture effect was interpreted as the specific site effect. The normal distribution of residuals
272 was verified using a Shapiro-Wilk test ($\alpha = 0.05$).
273 Plant cover, above- and below-ground biomasses, and SIR rates were compared between
274 local and exogeneous seeds at each sampling date using Mann-Whitney tests ($\alpha = 0.05$). Non-

275 metric multidimensional scaling (NMDS) ordination was used to visualize the vegetation
276 composition temporal dynamics across the three sites and seed mixture treatments, based on
277 the composition of the plant community (contribution of plant species to the total plot
278 vegetation cover averaged across the ten quadrats) from the three (Grand Tourmalet) or four
279 (Font Romeu, Les Angles) sampling years. Cover values of plant species were log-
280 transformed ($\log_{10}(D + 1)$) before analysis to reduce the weight of abundant species. Bray-
281 Curtis dissimilarity matrices were used and the NMDS was performed using 500 iterations.

282

283

284 **3- Results**

285

286 *3.1. Plant cover dynamics*

287

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

295 At Font Romeu, the plant cover rapidly developed in the local seed plot, with more
296 than 50 % covering after the first growing season and reaching 88 and 91 % cover after 3 and
297 4 years, respectively. Seedlings from exogeneous seeds suffered following a severe freezing

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

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

315 These differences in plant cover following the use of local or exogenous seed mixtures
316 were also visible in terms of percent surface covered by fine earth, and coarse elements
317 (stones) that resulted from both absence of vegetation cover and removal (by erosion) of fine
318 soil particles (**Supplementary material S4**). Indeed, the proportion (percent cover) of coarse
319 (>10 mm) elements was consistently 2.5 to 3 times higher with the use of exogeneous seeds
320 compared to that of local seeds. This was particularly critical at the Grand Tourmalet site. In

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

323

324 *3.2. Plant above and belowground biomasses*

325

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

334

335

336 *3.3. Plant community structure and diversity*

337

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

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

344 respectively, in Font Romeu, 19.3 and 16 in Grand Tourmalet, and 13.5 and 13.3 in Les
345 Angles (**Table 3**, see details in **Supplementary material S5**). The number of species that
346 were present in the initial seed mixtures and that were recorded in the plots ranged from 5.8
347 to 8 on average (among the 10 to 26 seeded species present in the mixtures). Finally,
348 numerous species recorded in the plots (45 to 78% of total species richness) were growing
349 spontaneously, *i.e.* were not present in the seed mixtures, for both LS and ES plots (**Table**
350 **3**).

351

352 3.4- Species composition :

353

354 The plots that had received local or exogenous seed mixtures exhibited strong difference in
355 plant composition across the three sites, and with a stronger site effect compared to the
356 sampling date effect (**Figure 2, Supplementary material S5**). Globally, the composition of
357 the plant cover strongly differed between LS (lower part of the NMDS plot) and ES plots
358 (top of NMDS plot, **Figure 2**). The composition of the plant covers fitted to some extent that
359 of the corresponding seed mixture especially at Les Angles and Grand Tourmalet, but to a
360 lower extent at Font Romeu. The plant community composition differed more in Font Romeu
361 (on the right of NMDS plot) compared to Les Angles / Grand Tourmalet where they were
362 more similar to each other (on the left). While some species were present at all sites in both
363 LS and ES plots (*Achillea millefolium*, *Agrostis capillaris*, *Atocion rupestre*, *Dactylis*
364 *glomerata*, *Festuca eskia.*, *Lolium perenne*, *Murbeckiella pinnatifida*, *Spergularia rubra*),
365 other species were recorded only in LS plots (*Festuca nigrescens*, accounting for 53.6 to
366 91.0% of the total plant cover), or in ES plots (*Festuca rubra*, with up to 77,7% plant cover,

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

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

389

390 In terms of origin of plant species, a larger proportion of plant cover came from
391 seeded species in LS compared to ES plots, especially at Font Romeu where a large
392 proportion of ES plant cover corresponded to spontaneous species (especially *Agrostis*
393 *capillaris* that accounted for 45 to 65.6% of plant cover across the sampling dates) (**Figure**
394 **3a**). Finally, the two meadow species that were added to the local seed mixture were not
395 always successfully recovered in the plots they were seeded in: at Font Romeu, *L. perenne*
396 rapidly disappeared after the second year while *T. repens* failed to establish despite its high
397 proportion in the LS mixture (**Supplementary material S5**).

398

399 *3.5- Plant cover composition by habitat type, forage value and species origin*

400

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

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

413 56.8% in LS compared to 13.1% in ES plot ($p < 0.001$). The large cover proportion of species
414 from meadows recorded in ES plots did not differ, however from that of LS plot (41.7 and
415 85.1% in LS and ES, respectively, $p = 0.109$) because of the large heterogeneity of plant
416 cover.

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

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

432

433 *3.6- Soil microbial activity*

434

435 Soil SIR rates differed between the three sites, with highest values at Grand Tourmalet site
436 with local seed mixtures ($11.05 \mu\text{g CO}_2\text{-C g}^{-1} \text{ soil h}^{-1}$ on average across the four years), and
437 lowest at Les Angles with exogenous seed mixture ($1.91 \mu\text{g CO}_2\text{-C g}^{-1} \text{ soil h}^{-1}$). A
438 significant effect of seed mixture was evidenced at Grand Tourmalet site only, with higher
439 SIR rates with local compared to exogenous seed mixture 2, 3 and 4 years after seeding
440 (**Figure 1c**). At Font Romeu and Les Angles, soil microbial activity (SIR) was comparable
441 in the plots with local and **exogenous** seed mixtures.

442

443 **4- Discussion**

444

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

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

457 cover in LS compared to ES plots did not always translate into higher plant biomass (except
458 at Grand Tourmalet). This is probably because high-elevation plants have low stature and
459 slow growth, compared to exogenous meadow species that are generally selected for their
460 high biomass production and fast growth. High-elevation herbaceous plants also display
461 functional traits that differ among species: they are generally smaller (Wright et al. 2017),
462 grow slowly because of the lower reserve in the seeds, and display thicker leaves and denser
463 tissues (Midono et al. 2019) compared to plants from lower elevation sites, probably in
464 response to low temperature and high irradiance. Both plant aerial parts, that protects the soil
465 surface against raindrop impact and surface run-off, and roots, that trap sediments and favour
466 infiltration, contribute to preventing soil erosion (Stokes et al. 2014, Vannopen et al. 2015).
467 LS plots were largely dominated by the tussock grass *Festuca nigrescens* (that accounted for
468 53.6 to 91.0 % of the plant cover according to sites and years), while ES plots were largely
469 dominated by *Festuca rubra*. These two graminoids largely contribute to soil aggregate
470 stability with their dense root system (Hudek et al. 2017). *Festuca nigrescens*, that is naturally
471 occurring sparsely in subalpine grasslands, is particularly appropriate for ski slopes and their
472 recreation operative conditions, with its low stature that stabilize the snowpack. However, it
473 was not easy to differentiate between *Festuca* species (especially between *F. nigrescens* and
474 *F. rubra* that look very similar). In the plots seeded with exogenous mixtures, part of the
475 plants recorded as *Festuca rubra* might be actually *Festuca nigrescens* that grows
476 spontaneously.

477

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

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

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

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

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

530

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

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

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

561 The use of local seed mixture also provided a higher forage plant cover compared to
562 that of exogenous seeds. *F. nigrescens*, that largely dominated the plant cover in LS plots, is
563 a good forage species with high productivity, as compared to other species from high-
564 elevation sites and/or to species that are conventionally used in revegetation. This is
565 important because the use of traditional, exogenous seed mixtures on ski runs generally
566 strongly decrease the pastoral value compared to non-disturbed grasslands ([Barrantes et al.,](#)
567 [2013](#)).

568

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

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

584

585

586 **Conclusions**

587

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

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

603

604

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612

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627

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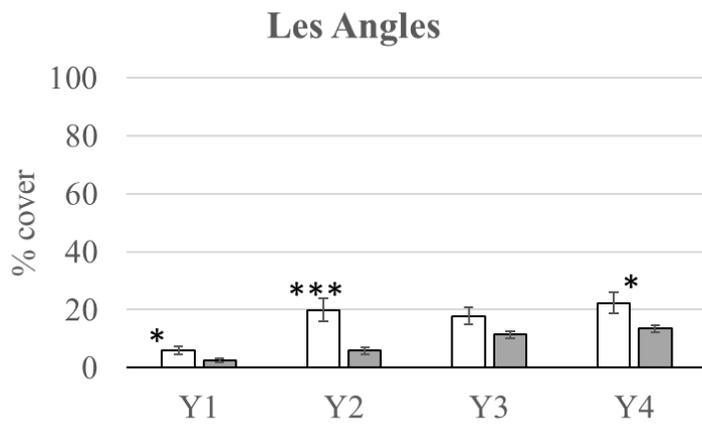
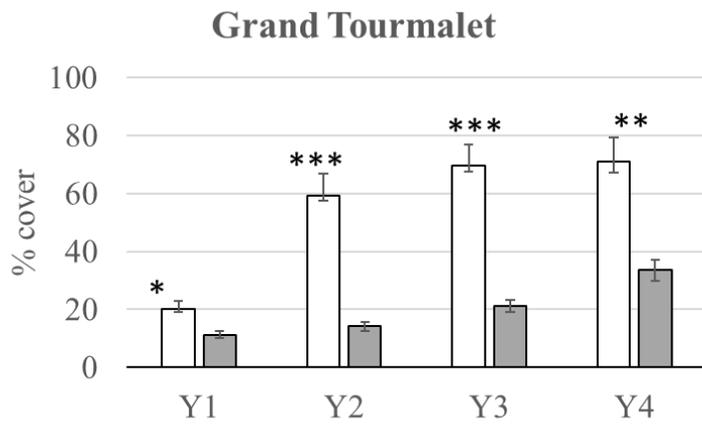
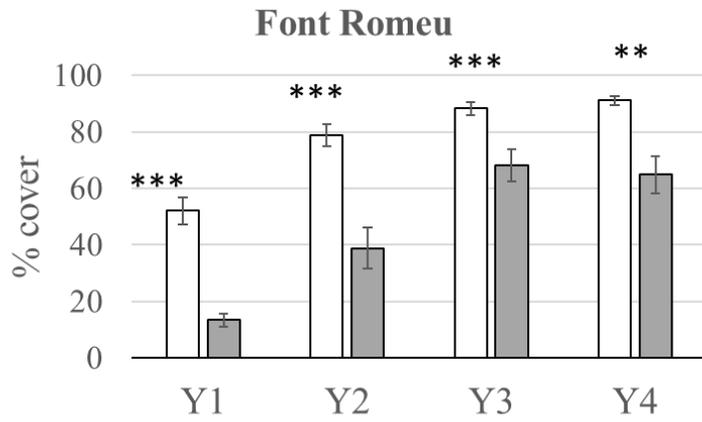
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795 **Figure 1- Dynamics of plant and soil parameters with local (white) and exogeneous**
796 **(grey) seed mixtures at the three reclamation sites 1, 2, 3 and 4 years after seeding.). ***
797 (for $p = 0.05$), ** (for $p < 0.01$), and *** (for $p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

800

801 **1a) total plant cover** (expressed as % of quadrat surface)

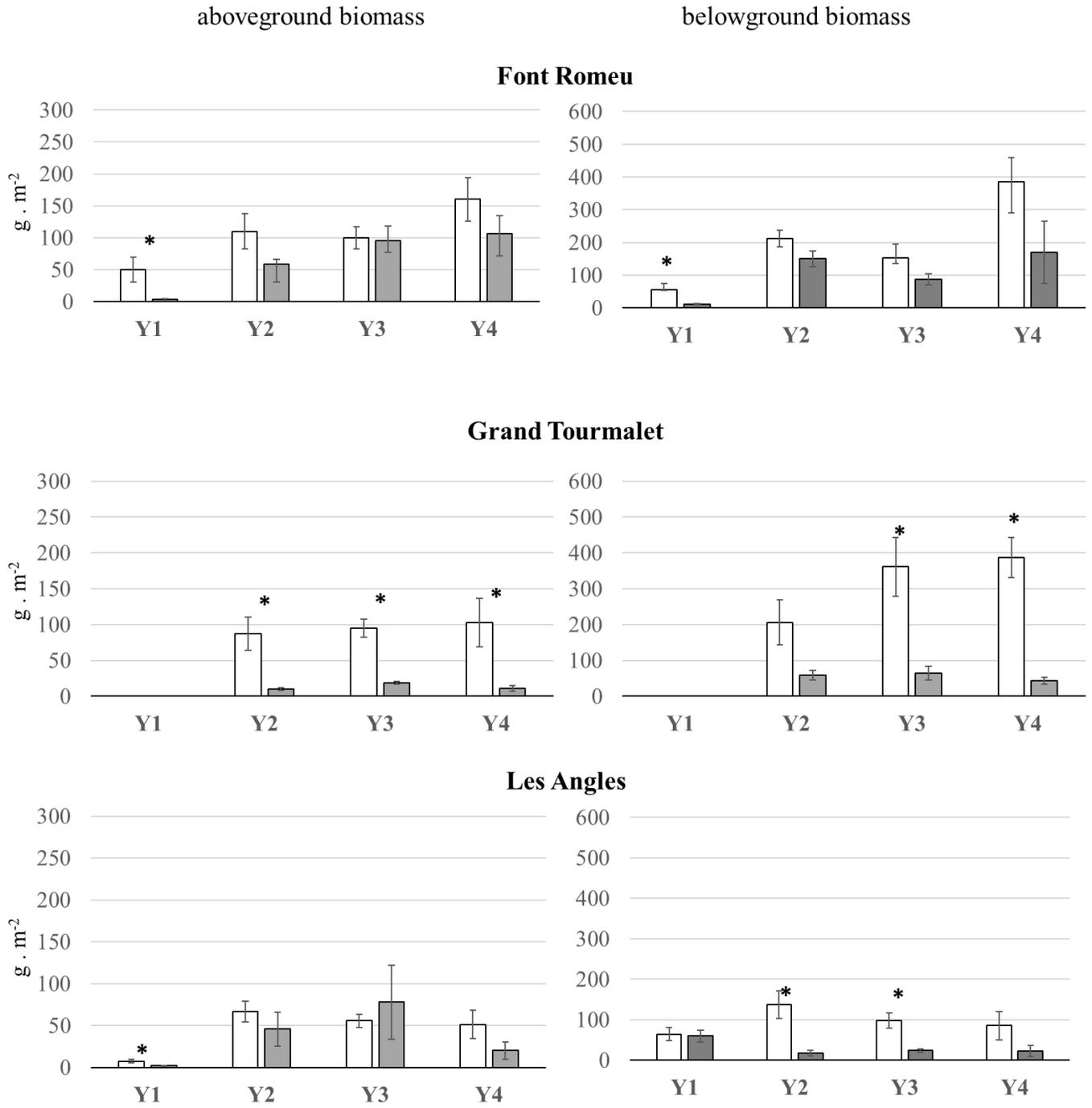
802 □ Local seed mixtures (LS) ■ Exogenous seed mixtures (ES)



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804 **1b) Plant aboveground and belowground biomasses**

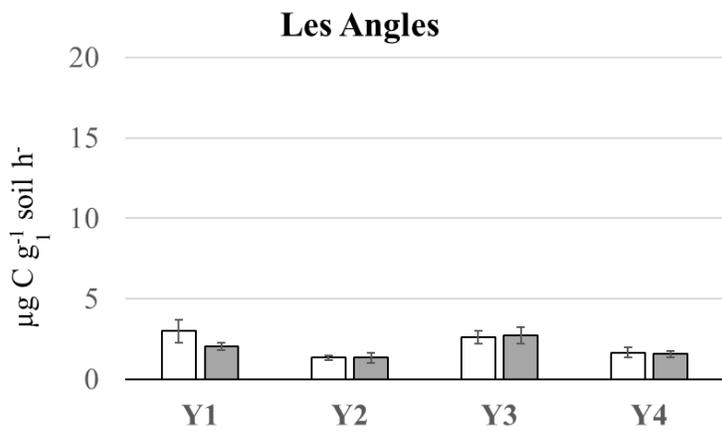
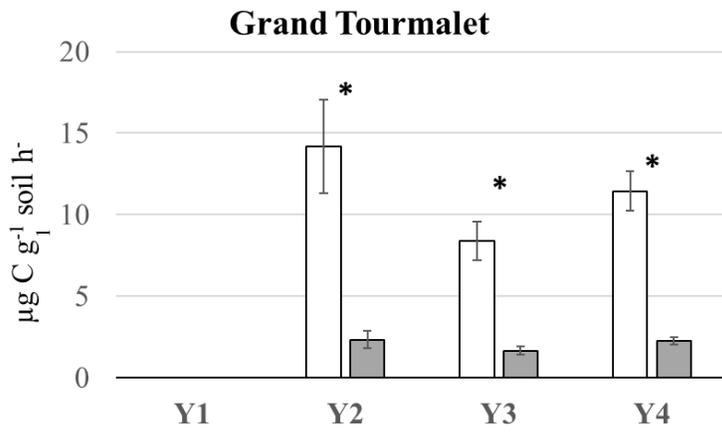
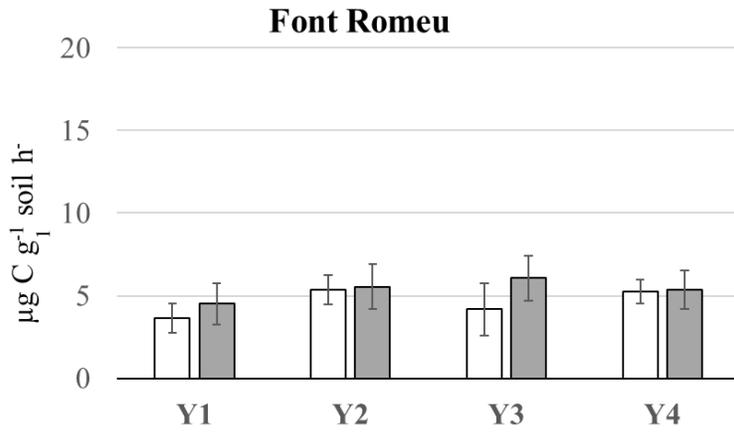
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 Local seed mixtures (LS)
 Exogenous seed mixtures (ES)



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807 **1c) Soil microbial activity (SIR rate)**

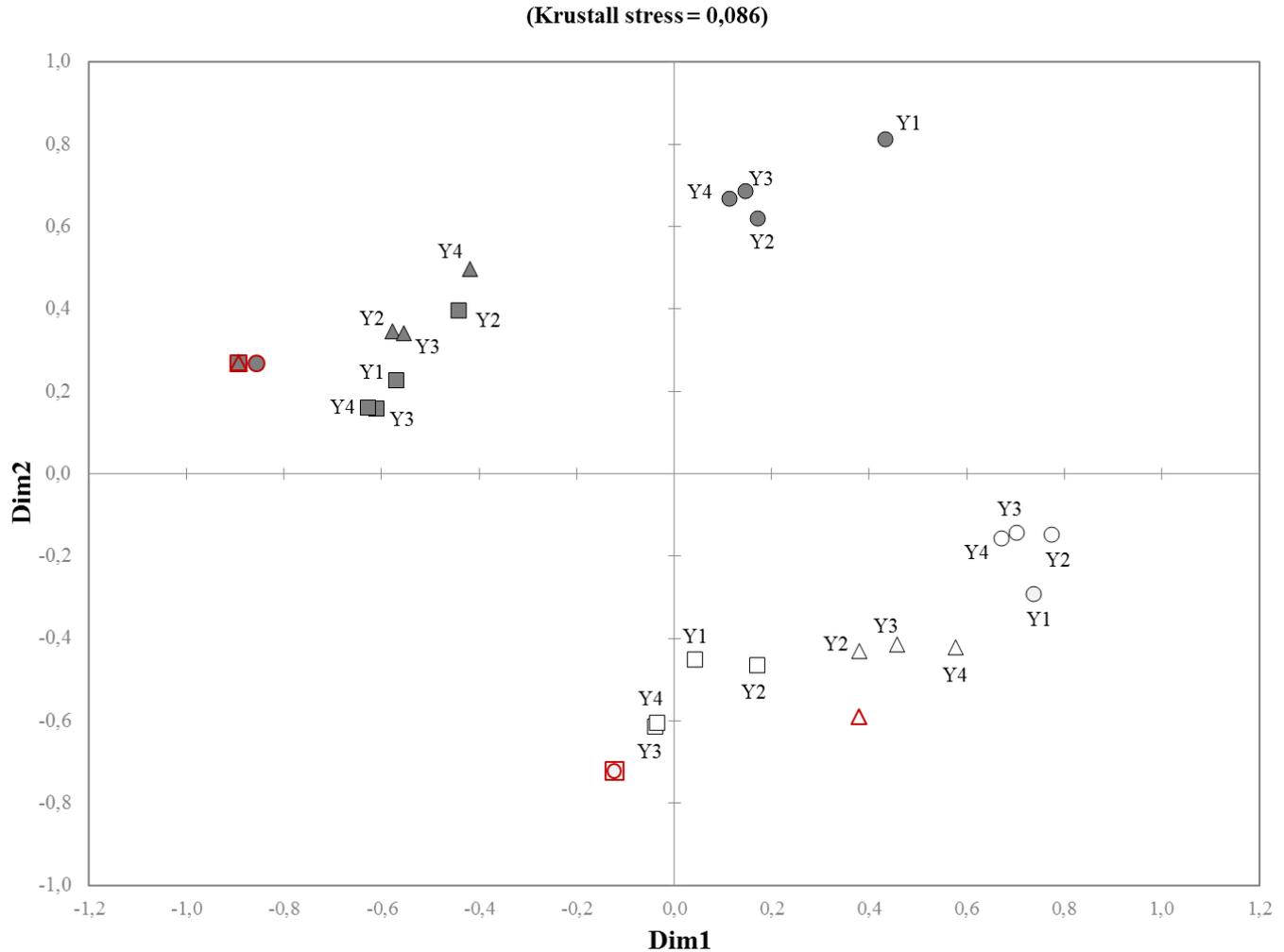
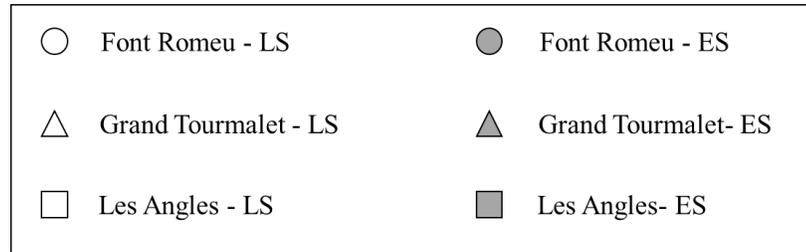
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810 **Figure 2- Nonmetric multidimensional scaling (NMDS) ordination of the plant**
 811 **community composition** at the three sites Font Romeu (FR, circle labels), Grand-Tourmalet
 812 (GT, triangle labels) and Les Angles (LA, square labels) in the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

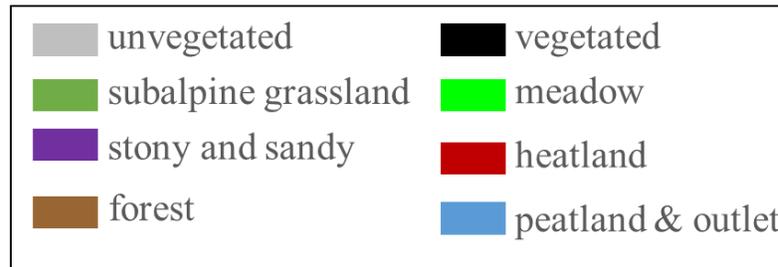
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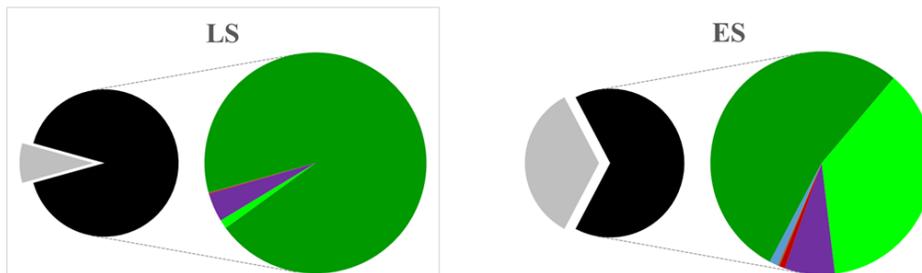
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822 **Figure 3- Vegetation at the three reclamation slope sites four years after seeding with**
 823 **local (LS) or exogeneous (ES) seed mixtures.**

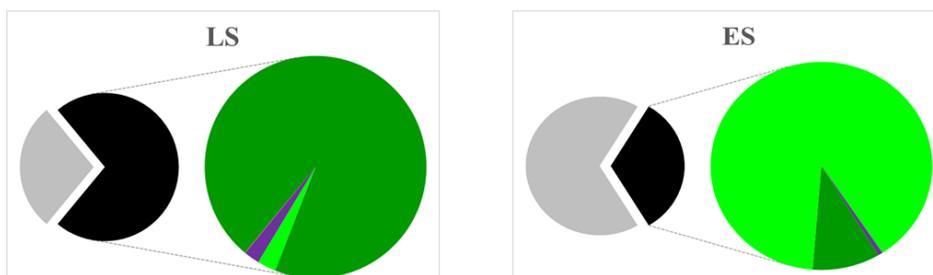
824 **3a) Composition of the plant covers by habitat types (average percent cover across the**
 825 **10 quadrats)**



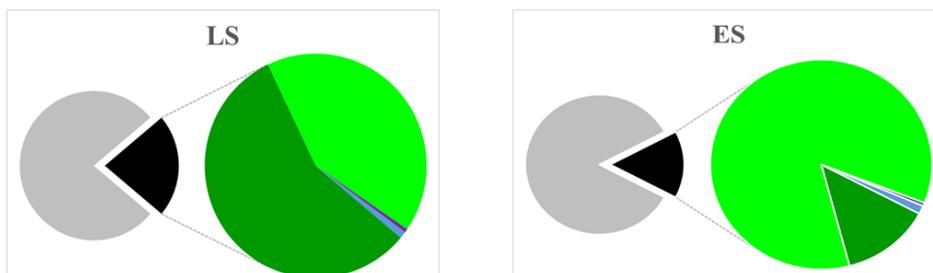
Font Romeu



Grand-Tourmalet



Les Angles



826

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	<i>Pinus uncinata</i> forest (less than 100 m away: <i>Nardion strictae</i>)	subalpine grassland (<i>Nardion strictae</i>)	<i>Pinus uncinata</i> forest (less than 100 m away: <i>Nardion strictae</i>)
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 m ² 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 m ² 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 m ² 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 m ²	240 m ²	350 m ²
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% P₂O₅, 5% K₂O, and 3% SO₃

^(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 \pm 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.

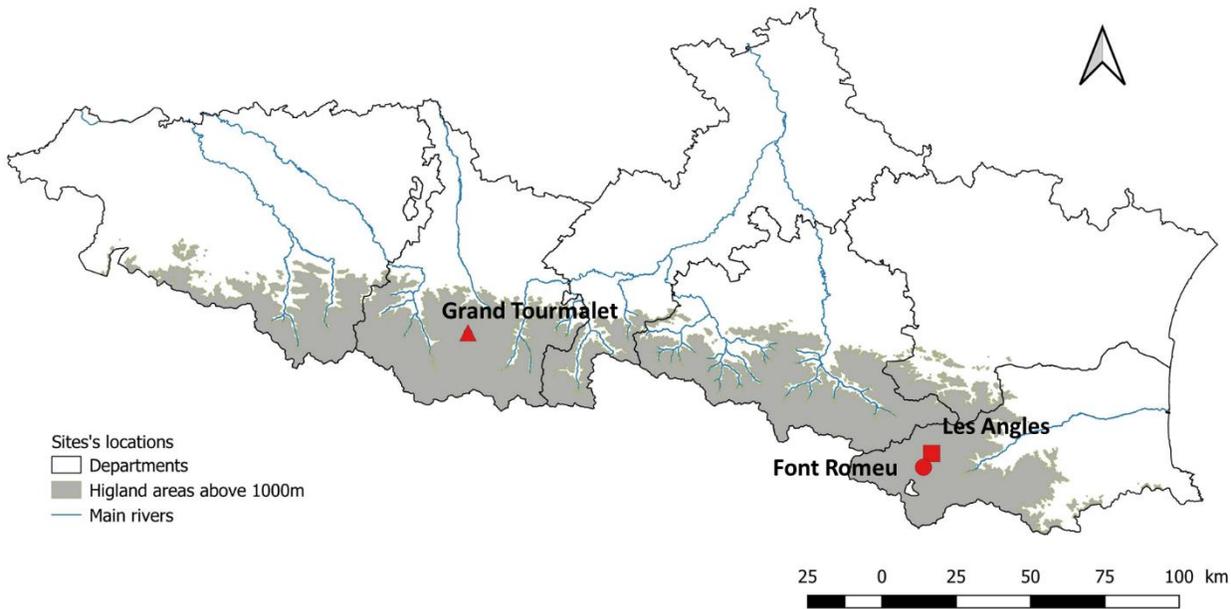
	Font Romeu LS	Grand Tourmalet LS	Les Angles LS	Font Romeu ES	Grand Tourmalet ES	Les Angles ES
in seed mixture	26	26	15	10	10	10
total	25.2 \pm 0.8	19.3 \pm 0.3	13.5 \pm 0.9	26.8 \pm 3.0	16.0 \pm 0.6	13.3 \pm 0.5
species in seed mix	6.8 \pm 0.8	7.7 \pm 0.3	6.0 \pm 0.0	5.8 \pm 0.5	8.0 \pm 0.0	5.8 \pm 0.3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

Table 3- Number of species present in the seed mixtures and recorded in the plots (mean values \pm 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 \pm 0.8	19.3 \pm 0.3	13.5 \pm 0.9	26.8 \pm 3.0	16.0 \pm 0.6	13.3 \pm 0.5
species in seed mix	6.8 \pm 0.8	7.7 \pm 0.3	6.0 \pm 0.0	5.8 \pm 0.5	8.0 \pm 0.0	5.8 \pm 0.3
'target' species	21 \pm 0.9	17.0 \pm 0.0	6.3 \pm 0.8	18.5 \pm 2.4	8 \pm 0.6	4.8 \pm 0.5
spontaneous species	18.5 \pm 0.9	11.7 \pm 0.3	7.5 \pm 0.9	21 \pm 3.2	8 \pm 0.6	7.5 \pm 0.5

Supplementary material

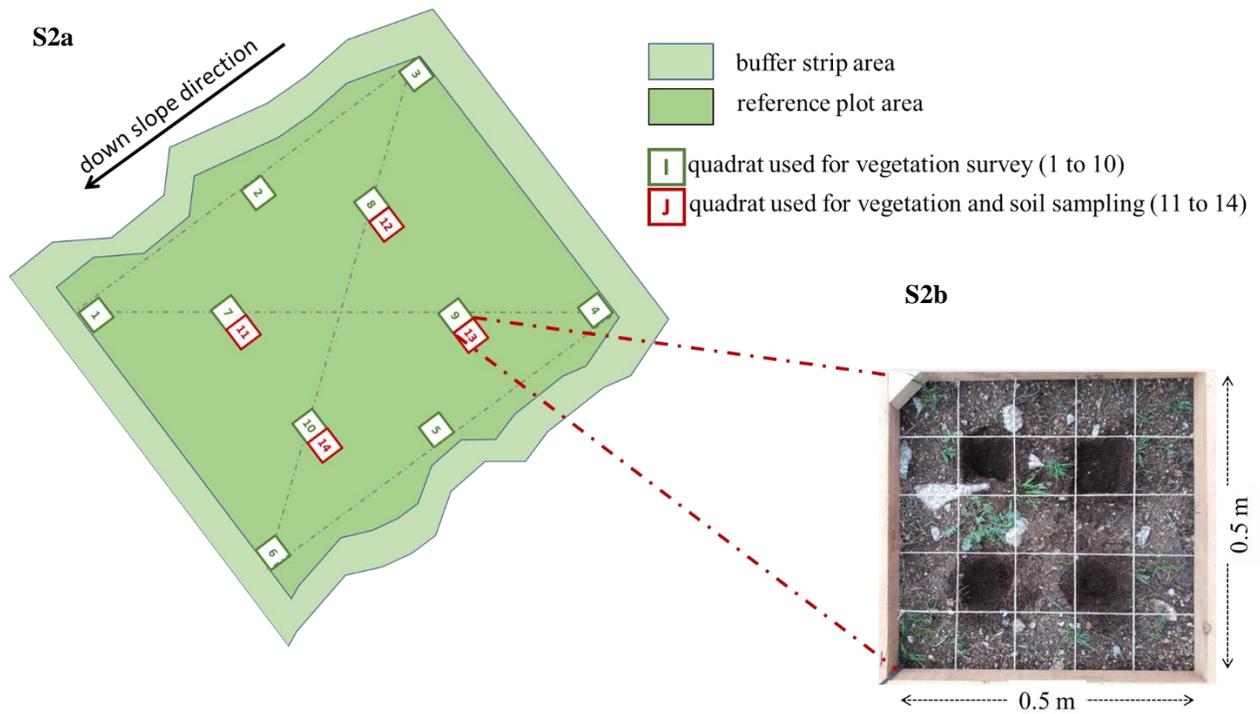
Supplementary material S1- Location of the sites



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.



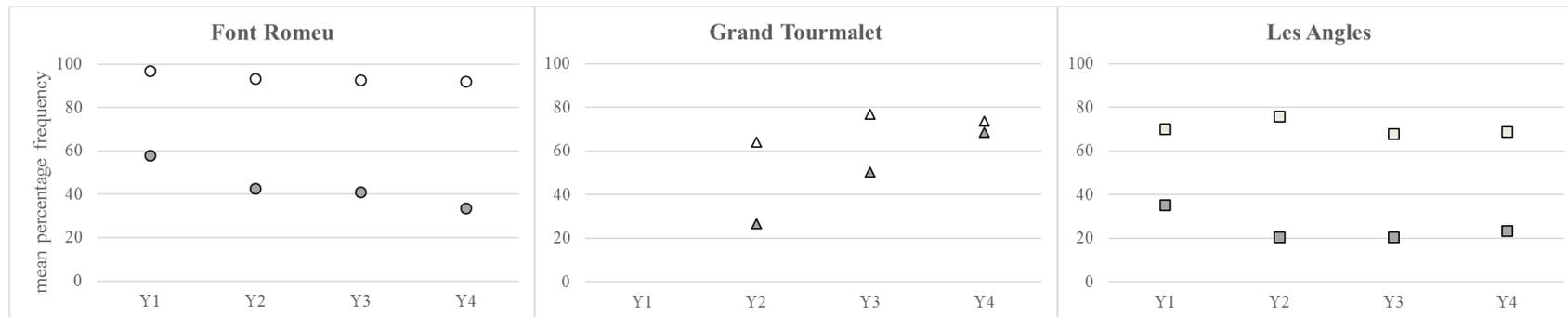
Supplementary material S3 –Poaceae percentage frequencies in plots seeded with local or exogenous seed mixtures at Font Romeu, Grand Tourmalet and Les Angles.

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).

Species	sp	Local seed mixture											Exogenous seed mixture											
		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	
<i>Agrostis capillaris</i>	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%	
<i>Briza media L.</i>	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%	0,0%
<i>Dactylis glomerata</i>	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%	
<i>Festuca eskia</i>	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%	
<i>Festuca nigrescens</i>	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%	0,0%
<i>Festuca rubra</i>	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%	
<i>Koeleria pyramidata</i>	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%	0,0%
<i>Lolium perenne</i>	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%	
<i>Nardus stricta</i>	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%	0,0%
<i>Phleum pratense</i>	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%	
<i>Poa alpina</i>	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%	0,0%
<i>Poa trivialis</i>	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%	0,0%
<i>Schedonorus arundinaceus</i>	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: $\sum_i^j (\text{percentage frequency}(i) * \frac{\text{cover}(i)}{\sum_i^j \text{cover}(i)})$, with $\text{cover}(i)$ 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.

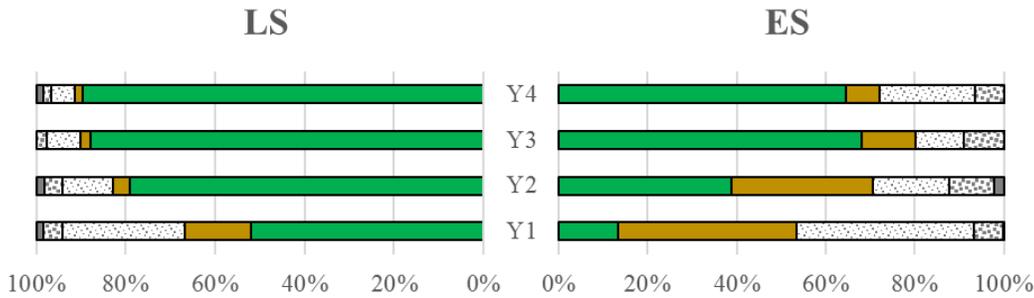


This graph shows that the mean percentage frequency for Poaceae is higher in the plots seeded with local (LS) compared to exogenous (ES) seed mixtures at the three experimental sites. At Font Romeu and Les Angles, Poaceae mean percentage frequency was at least two times higher in LS compared to ES plots, 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.

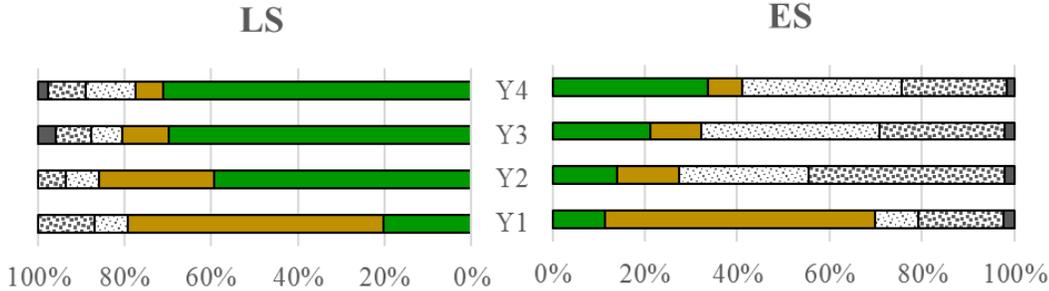
Supplementary material S4- Estimation of plot covers following local (LS) and exogenous (ES) seed mixture seeding at Font Romeu, Grand Tourmalet and Les Angles ski slopes. Plant cover, FE: fine earth cover (%), CE<10: fine (< 10 mm) element cover (%), CE>10: coarse (> 10 mm) element cover (%), and others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



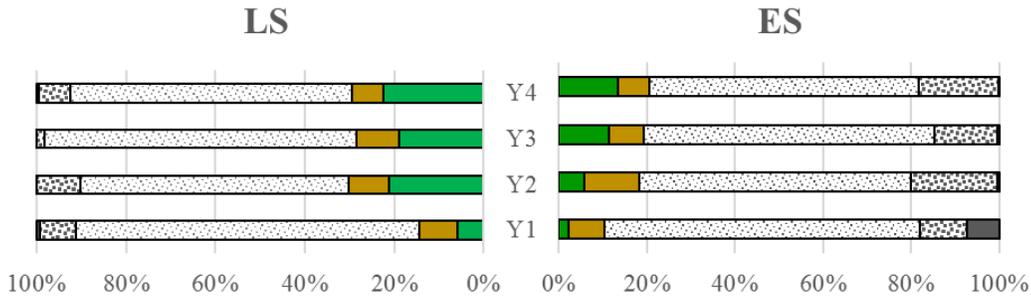
Font Romeu



Grand Tourmalet



Les Angles



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 <i>F value</i>	date <i>F value</i>	Seed mixt. X date <i>F value</i>
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 <i>F value</i>	date <i>F value</i>	Seed mixt. x date <i>F value</i>
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.

Species present in seed mixtures	Family	Typical habitat	sp	Forage interest	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	
					Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y1	Y2	Y3	Y4	Y2	Y3	Y4	Y1	Y2	Y3	Y4							
<i>Achillea millefolium</i> 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			
<i>Anthoxanthum odoratum</i> 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	0	0	0	0	0	0	
<i>Avenella flexuosa</i> (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	0	0	0	0	0	
<i>Bistorta officinalis</i> 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	0	0	0	0	0	
<i>Briza media</i> 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	0	0	0	0	0	0	
<i>Carex brizoides</i> 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	0	0	0	0	0	0	
<i>Carex nigra</i> (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	0	0	0	0	0	
<i>Conopodium majus</i> (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	0	0	0	0	0	
<i>Dactylis glomerata</i> 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			
<i>Dianthus deltoides</i> 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	0	0	0	0	0	
<i>Festuca eskia</i> 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	0	4.10	0			
<i>Festuca nigrescens</i> 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	0	0	60.73	79.10	0	0	
<i>Festuca rubra</i> L.	Poaceae	Meadow	Fr	Forage	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	0	0	0	0	30.00	25.00
<i>Galium verum</i> 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	0	0	0	0	0	
<i>Jasione laevis</i> 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	0	0	0	0	
<i>Koeleria pyramidata</i> (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	0	0	3.64	0	0	0	
<i>Lolium perenne</i> 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			
<i>Lotus corniculatus</i> 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	0	0	1.00	0	
<i>Medicago sativa</i> 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	0	0	1.00	0	
<i>Nardus stricta</i> 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	0	0	2.60	5.30	0	0	
<i>Onobrychis vicifolia</i> 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	0	0	10.00	5.00	
<i>Phleum pratense</i> 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			
<i>Plantago lanceolata</i> 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			
<i>Plantago monsperma</i> 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	0	0	0.20	0	
<i>Poa alpina</i> 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	0	0	1.20	0	0	
<i>Poa trivialis</i> 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	0	0	1.05	0	0	0	
<i>Poterium sanguisorba</i> 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	0	6.00	3.00			
<i>Ranunculus acris</i> 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	0	0	1.30	0	0	0	
<i>Rhinanthus minor</i> 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	0	0.74	0	0	0	
<i>Schedonorus arundinaceus</i> (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			
<i>Scorzoneroides pyrenaica</i> (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	0	0.30	0	0	0	
<i>Taraxacum</i> 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	0	0.01	0	0	0	
<i>Tragopogon pratensis</i> L.	Asteraceae	Meadow	Ttp	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	0	0.01	0	0	0	
<i>Trifolium pratense</i> 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	0	0.30	0	0	0	
<i>Trifolium repens</i> 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			
<i>Vicia sepium</i> 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	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.

Species present in seed mixtures	Family	Optimum natural habit	sp	Forage interest
<i>Agrostis capillaris</i> L.	Poaceae	Subalpine grassland	Ac	Forage
<i>Alchemilla alpina</i> L.	Rosaceae	Stony and sandy habitat	Aa	Non forage
<i>Anemone nemorosa</i> L.	Ranunculaceae	Meadow	An	Non forage
<i>Atocion rupestre</i> (L.) B.Oxelmann	Caryophyllaceae	Stony and sandy habitat	Ar	Non forage
<i>Calluna vulgaris</i> L. Hull	Ericaceae	Heatland	Cv	Non forage
<i>Carex caryophyllea</i> Latourr.	Cyperaceae	Subalpine grassland	Cc	Non forage
<i>Cirsium eriophorum</i> (L.) Scop.	Asteraceae	Peatland & outlet	Ce	Non forage
<i>Coincya monensis subsp. cheiranthos</i> (Vill.)	Brassicaceae	Stony and sandy habitat	Cmo	Non forage
<i>Crocus nudiflorus</i> Sm.	Iridaceae	Subalpine grassland	Crn	Non forage
<i>Cytisus oromediterraneus</i> Rivas Mart. & al.	Fabaceae	Heatland	Co	Non forage
<i>Galium pumilum</i> Murray	Rubiaceae	Subalpine grassland	Gap	Non forage
<i>Galium saxatile</i> L.	Rubiaceae	Subalpine grassland	Gas	Non forage
<i>Gnaphalium sylvaticum</i> L.	Asteraceae	Subalpine grassland	Gns	Non forage
<i>Hypochaeris radicata</i> L.	Asteraceae	Meadow	Ha	Non forage
<i>Leontodon hispidus</i> L.	Asteraceae	Meadow	Lh	Non forage
<i>Leucanthemum vulgare</i> Lam.	Asteraceae	Meadow	Lv	Non forage
<i>Linaria repens</i> (L.) Mill.	Plantaginaceae	Stony and sandy habitat	Lr	Non forage
<i>Luzula campestris</i> (L.) DC.	Juncaceae	Subalpine grassland	Luc	Non forage
<i>Meum athamanticum</i> Jacq.	Apiaceae	Subalpine grassland	Ma	Non forage
<i>Murbeckiella pinnatifida</i> (Lam.)	Brassicaceae	Stony and sandy habitat	Mp	Non forage
<i>Paronychia polygonifolia</i> (Vill.) DC.	Caryophyllaceae	Stony and sandy habitat	Pap	Non forage
<i>Pinus nugo</i> subsp. <i>uncinata</i> (Ramond ex DC.) Domin	Pinaceae	Forest	Pim	Non forage
<i>Plantago maritima</i> L.	Plantaginaceae	Subalpine grassland	Pma	Forage
<i>Pilosella lactucella</i> (Wallr.) P.D.Sell & C.West	Asteraceae	Subalpine grassland	Pil	Non forage
<i>Pulsatilla alpina</i> (L.) Delarbre	Ranunculaceae	Subalpine grassland	Pua	Non forage
<i>Ranunculus pyrenaicus</i> subsp. <i>pyrenaicus</i> L.	Ranunculaceae	Subalpine grassland	Rp	Non forage
<i>Rumex acetosa</i> L.	Polygonaceae	Meadow	Rat	Non forage
<i>Rumex acetosella</i> L.	Polygonaceae	Stony and sandy habitat	Ral	Non forage
<i>Sagina saginoides</i> subsp. <i>pyrenaica</i> (Rouy) Font Quer	Caryophyllaceae	Subalpine grassland	Ss	Non forage
<i>Sceleranthus perennis</i> L.	Caryophyllaceae	Stony and sandy habitat	Spe	Non forage
<i>Sesamoides pygmaea</i> (Scheele) Kuntze	Resedaceae	Stony and sandy habitat	Sep	Non forage
<i>Sisymbrium austriacum</i> Jacq.	Brassicaceae	Peatland & outlet	Sia	Non forage
<i>Spergularia rubra</i> (L.) D. Dietr.	Caryophyllaceae	Stony and sandy habitat	Sr	Non forage
<i>Trifolium alpinum</i> L.	Fabaceae	Subalpine grassland	Ta	Forage
<i>Vaccinium myrtillus</i> L.	Ericaceae	Peatland & outlet	Vm	Non forage
<i>Veronica arvensis</i> L.	Plantaginaceae	Stony and sandy habitat	Va	Non forage
<i>Veronica fruticans</i> Jacq.	Plantaginaceae	Stony and sandy habitat	Vf	Non forage
<i>Viola reicheinbachiana</i> Jord. ex Boreau	Violaceae	Forest	Vr	Non forage

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		
0,87	3,65	8,24	8,29	0,07	0,06	0,06	0	0,97	0	0	0	65,59	56,20	45,03	45,02	0	0	0	1,07	5,12	0,28	0	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,56	0,55	0	0	0	0	0	0	0	
0	0	0,05	0,06	0	0	0	0	0	0	0	0	0,56	0	0	0	0	0	0	0	0	0	0	
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		
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	0,07	0,76	0	0	0	0	0	0		
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		
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		
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		
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		
0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,15	0	0	0	0	0	0	0		
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		
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		
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		
0	0	0	0	0	0	0	0	0,18	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	0,07	0,15	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	0,26		
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		
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		
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		
0	0	0	0	0	0	0	0	0	0	0	0	0	0,07	0,15	0	0	0	0	0	0	0		
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		
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		
0	0,05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
0	0	0	0	0,34	0,14	0,06	0	0	0	0	0	0	0	0	0	0,12	0	0	0	0	0		
0	0	0	0	0	0	0	1,94	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
0,16	0,79	0,23	0,40	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	0		
0	0	0	0	0,07	0,14	0	0	0	0	0	0	0	0	0,27	0	0	0	0	0	0	0		
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		
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		
0	0	0	0	0	0	0	0	0,18	0,75	0,63	0	0	0	0	0	0	1,20	0	0	0	0		
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		
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		
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		
0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
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		
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		
nombre 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		

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

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



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



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



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