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1 **Mountain grassland restoration using hay and brush material transfer combined with temporary**
2 **wheat cover**

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15 **Short title:** Restoring mountain grasslands by propagule transfer

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21 **Abstract**

22 Mountain grassland restoration success may be hampered by limited seed dispersal and poor
23 soil seed banks of many grassland species. These constraints can be overcome by actively
24 introducing propagules from nearby non-degraded communities. We tested different
25 restoration techniques in order to understand the mechanisms favouring target species
26 seedling recruitment and establishment. In five degraded mountain grasslands, we analysed (i)
27 the effect of two techniques increasingly used in ecological restoration to overcome low seed
28 dispersal: transfer of brush-harvested seed material and hay transfer, and (ii) the potentially
29 facilitative effect of a temporary plant cover (common wheat) on the recruitment of transferred
30 brush-harvested propagules. We found that both propagule transfer techniques were
31 successful in establishing plant species of the donor community with an increase of plant
32 species richness, cover and abundance of transferred species. Hay transfer was more efficient
33 in transferring species of the donor grassland than brush-harvested material transfer. Brush-
34 harvested material transfer only increased abundance and cover of donor grassland species
35 when sown together with wheat. The results indicated that hay mulch favoured seedling
36 recruitment of target species, and that propagule transfer without hay mulch needs to be
37 compensated by additional temporary plant cover in order to create favourable conditions for
38 seedling recruitment. A comparison with best reference communities for each restoration
39 grassland confirmed that hay transfer and brush material transfer with wheat sowing were
40 successful in driving plant community composition towards the desired reference state. In
41 conclusion, restoration of mountain grasslands with shallow and stony soils clearly benefits
42 from a facilitative effect of dead (hay) or living (wheat) vegetation cover.

43

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45 **Keywords**

46 Semi-natural montane grasslands, Seedling recruitment, Nurse crop, Erosion control, Mulch
47 effect, Facilitation

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64 1. Introduction

65 Grassland ecosystems represent 25% of terrestrial biomes (Blair et al., 2014; Wilsey, 2020) and
66 are essential habitats for the conservation of biodiversity and associated ecosystem services
67 (Stoate et al., 2009; Amiaud & Carrère, 2012; Valkó et al., 2016). Since the 1980ies, the
68 conservation of species-rich semi-natural grasslands has become a major concern in Europe.
69 Most European semi-natural grasslands were integrated in the habitat management Natura
70 2000 network in order to stop habitat degradation and to re-establish grassland species
71 diversity using ecological restoration approaches (Wilsey, 2020).

72 Successful grassland restoration may be primarily hampered by limited dispersal
73 capacity and/or poor soil seed banks of many grassland species, and by a grazing management
74 favouring clonal reproduction over sexual reproduction (Halassy et al., 2016; Török et al., 2018).
75 These constraints are well documented and can be overcome by actively introducing
76 propagules (Kiehl et al., 2010; Scotton et al., 2012; Hölzel et al., 2012). The use of native plant
77 species of local origin is recommended to assure adaptation to local environmental conditions
78 and to maintain genetic diversity (Vander Mijnsbrugge et al., 2010; Bucharova et al., 2019).
79 Consequently, transferring local seeds from nearby non-degraded communities is increasingly
80 used in ecological restoration (Scotton, 2019). Diverse techniques are currently applied
81 depending on specific environmental conditions at restoration and donor sites (Kiehl et al.,
82 2010; Hedberg & Kotowski, 2010). The increasing number of studies illustrates the scientific
83 interest in comparing restoration effectiveness of various seed harvesting and transfer
84 techniques (Scotton & Ševčíková, 2017), such as hay transfer vs. sowing of seed mixtures
85 (Auestad et al., 2015; Kövendi-Jakó et al., 2019), brush material vs. green hay transfer (Albert

86 et al., 2019), or sowing combined with various additional treatments (Török et al. 2012;
87 Pawluśkiewicz et al., 2019; Havrilla et al., 2020).

88 In our study, we compared the restoration effectiveness of two mechanical harvesting
89 techniques increasingly used in mountain grassland restoration: the transfer of brush-
90 harvested seed material and the transfer of dry hay both collected from the same donor site
91 located close to the degraded grasslands. The brush harvester strips and aspirates the plant
92 material without cutting (Scotton et al., 2012). The harvested brush material comprises seeds
93 but also vegetative parts of fruits and, to a lesser degree, other vegetative material. Low-
94 growing and less abundant species may be under-represented in this material (Edwards et al.,
95 2007; Scotton et al., 2009; Wagner et al., 2020), but brush harvesting allows concentrating
96 seeds thus reducing humidity and facilitating storage. It also reduces the mulch layer that may
97 hamper germination (Mollard et al., 2014). Dry hay transfer involves cutting of plant material
98 close to the soil surface, drying it on the field before storage and spreading it on the restoration
99 site. The higher vegetative biomass compared with brush material may hamper germination
100 but protects seedlings against high solar radiation, drought and soil erosion (Eckstein & Donath,
101 2005; Graiss & Krautzer, 2011; Havrilla et al., 2020).

102 As seedling recruitment and establishment are important constraints in semi-natural
103 grassland restoration (Öster et al., 2009), we also tested whether simultaneous transfer of
104 brush material and sowing of an annual plant species may compensate for the absence of a
105 protecting mulch layer. Such annuals provide temporary living cover that may facilitate seedling
106 recruitment and establishment (Padilla et al., 2006; Wright et al., 2014). Similarly to hay mulch,
107 a living cover may, however, increase root and light competition (Donath et al., 2006). We
108 tested a mix of two lowland varieties of common wheat *Triticum aestivum* as a facilitative
109 species. These varieties were expected to disappear within a couple of years since climatic

110 conditions of our mountain study sites limit their seed production and self-sowing. *Triticum*
111 cover may reduce soil erosion, an important criterion for the functionality of restoration
112 measures. Such soil stabilisation and erosion control are particularly important in mountain
113 grasslands on slopes facing a high risk of soil loss and propagule run-off (Huc et al., 2018;
114 Scotton, 2019).

115 In order to understand the underlying mechanisms of seedling recruitment and
116 establishment, we analysed first-year seedling abundance and second-year cover, respectively.
117 To determine which technique is the most appropriate in mountain grassland restoration, we
118 addressed the following questions: (1) Which method of plant material transfer is most
119 successful in establishing species transferred from the donor community? (2) Does sowing of
120 wheat improve the seedling establishment of brush material? (3) Do transfer techniques and
121 wheat sowing increase the similarity between restored and reference communities? (4) What
122 is the influence of these treatments on soil erosion?

123

124

125 **2. Material and methods**

126 **2.1. Study area**

127 The study area was the upper Durance valley in the Southern French Alps. The five selected
128 restoration sites were degraded by the construction of a high-voltage transmission line
129 involving the creation of access tracks and working platforms. The construction work locally
130 destroyed the vegetation and affected the soil structure. The study zone extends over about
131 100 km, from L'Argentière-la-Bessée in the north to La-Bâtie-Neuve in the south (44°78'78"N,
132 6°59'41"E; 44°57'93"N, 6°20'77"E). The study sites are located on slopes above the Durance
133 valley, at an elevation of 1060 m to 1320 m above sea level. They are characterised by a

134 subcontinental climate, with an average annual temperature of 8.7°C and an annual rainfall of
135 740 mm (Embrun meteorological station, annual temperature corrected for an altitudinal
136 difference of roughly 2°C). Dry to mesophilic grasslands occur at sites managed by grazing or
137 mowing. Most of these surrounding non-degraded grasslands are priority habitats of Natura
138 2000: "Semi-natural dry grasslands of Festuco-Brometalia and scrubland facies on limestone"
139 (N6210, European habitat directive 92/43/EEC; Calaciura & Spinelli, 2008). The five restoration
140 sites used for the experiments were former access tracks and working platforms, and
141 restoration goal was the re-establishment of typical Festuco-Brometalia grasslands. Traditional
142 management by grazing was re-introduced.

143

144 *2.2. Donor and reference sites*

145 One typical non-degraded Mesobromion grassland of the study area was chosen as donor site
146 for harvesting plant material. The site was located in Freissinières (44°73'61"N; 6°56'72"E) at
147 an elevation of 1100 m and a 3° south-west-facing slope. Two harvest techniques were applied,
148 brush harvesting and traditional haymaking. The brush material was harvested on 13 July 2018
149 using a brush harvester mounted on a quad and equipped with an integrated vacuum system.
150 On a surface of 4000 m², 2.6 kg of brush material was obtained. The harvested material
151 comprised seeds (60 % of total mass) and vegetative parts (40 %). Seeds were counted in 10
152 subsamples of 0.5 g harvested material revealing an average density of 887 seeds/g. Hay was
153 cut at 15 July 2018 on an additional area of 800 m² at the same donor site using a rotary mower.
154 Harvest conditions were dry and warm without rainfall during the previous days. The hay was
155 dried for two days on the harvested grassland and was baled in five bales of 7.5 kg (45 × 30 ×
156 75 cm) for a total of 37.5 kg, with approximately 1 % of seeds in the total raw material. Brush

157 material and hay were kept for three months at room temperature under dry and dark
158 conditions.

159 Although the donor site reflected the medium environmental conditions of the five
160 restoration sites we identified “best references” for each site to evaluate restoration success.
161 Since best reference sites are not always the closest ones (Durbeq et al., 2020), we surveyed
162 eighteen non-degraded grasslands along the new electricity line. These potential references
163 included the donor site and were located at the same altitudinal belt as restoration sites (1000
164 – 1400 m). Soil and microclimatic conditions measured at restoration sites and potential
165 reference communities were used to identify the best references of each restoration site
166 according to Durbeq et al., (2020, methodology).

167

168 **2.3. Experimental design**

169 At the five restoration sites, we repeated the following five treatments in 4 m × 4 m plots:
170 control without hay or brush material transfer (‘Control’), hay transfer (‘Hay’), brush material
171 transfer (‘Seed’), wheat sowing (‘Triticum’) and both brush material and wheat seed addition
172 together (‘Triticum + Seed’). The restoration sites that were already colonized by spontaneous
173 vegetation (mainly *Chenopodium album* L. and *Atriplex patula* L.) were mown before the set-
174 up of the experiments and they were then extensively grazed in spring and autumn. The
175 position of the five treatments was randomised within sites.

176 In October 2018, 6.5 g/m² of harvested brush material was spread in the brush material
177 treatments, corresponding to 3.75 g/m² of seed and 5765 seeds/m². The chosen seed density
178 is a little higher than recommended for lowland grasslands and lower than usually sown in
179 alpine grasslands (Kiehl et al., 2010; Scotton et al., 2012; Koch et al., 2015). The brush material

180 was pressed to the ground using a lawn roller. In the hay transfer treatment, a bale of hay of
181 7.5 kg was spread (0.5 kg/m²) on each plot. The amount of hay was adjusted to an estimated
182 seed content of 1% (Scotton et al., 2012) corresponding to roughly 5 g/m² of seeds. The hay
183 was pressed to the ground by the wheels of tractor in order to maintain hay on the ground. The
184 sown wheat treatment was a mixture of two local lowland winter wheat (*Triticum aestivum*)
185 varieties, “Meunier d'Apt” and “Saissette de Provence”. These early lowland varieties are not
186 well adapted to high altitude resulting in low seed production and a rapid decline during
187 mountain grassland succession. The seed density was adjusted to 9 g/m². Like for the brush
188 material transfer, a lawn roller was used to improve seed adhesion to the ground. Controls
189 were not sown but they were also rolled.

190

191 **2.4. Data collection**

192 *2.4.1. Vegetation surveys in donor and reference grasslands*

193 In the donor grassland, vegetation surveys were conducted on 29 June 2018, and the
194 occurrence of mature seeds was evaluated for each plant species at the harvest date. Surveys
195 were used to establish a list of 37 potentially transferred species (hereafter: transferred
196 species). The vegetation surveys of the eighteen potential reference sites were conducted
197 between 21 June and 5 July 2018 by visual estimation of plant cover for each species in quadrats
198 of 2 m × 2 m. In the donor grassland, five quadrats were sampled, and three in each of the
199 other potential reference grasslands. Additionally, we monitored seed maturity in each plant
200 species at the day of harvest.

201

202 *2.4.2. Germination test in a greenhouse*

203 In November 2018, brush material and hay were spread in an unheated greenhouse to evaluate
204 and compare the germination potential of seeds in brush material and hay. Harvested brush
205 material and dry hay were sown to ten trays (0.03 m²) filled with standard potting soil substrate
206 (mixture of 1/3 vermiculite and 2/3 of sterile peat). Five trays received 0.54 g of brush material
207 corresponding to 18g/m² of seeds, and five trays received 12.5 g of hay corresponding to 4
208 g/m² of seed material according to an estimated seed content of 1%. The trays were regularly
209 watered, and germinations identified and removed until April 2019.

210

211 *2.4.3. Seedling abundance and vegetation surveys in grasslands under restoration*

212 To measure seedling abundance, plant number was counted in three quadrats of 40 ×
213 40 cm placed along the diagonal of each plot in June 2019, at the five restoration sites. Since it
214 was not possible to distinguish seedlings and plants re-sprouting from belowground organs, the
215 seedling counts may include stems or ramets of vegetative regeneration. We considered all
216 reproducing plant species of the donor site as transferred although some of them also occurred
217 in the control plots of sites under restoration, indicating their presence in the soil seed bank or
218 seed rain. In June 2020, the cover of plant species was measured following the same protocol
219 as in the potential reference grasslands: in each plot, one quadrat of 2 m × 2 m was sampled.

220

221 *2.4.4. Erosion monitoring*

222 To evaluate the effect of the different treatments on soil erosion, we measured erosion
223 according to Feret & Sarrailh ([2005](#)) at four restoration sites (at one site, the permanent points
224 were accidentally removed in autumn 2019 not allowing any analysis). The device comprised a

225 1.5 m long aluminium bar and two 0.5 m long iron poles fixed in the ground of each plot. These
226 iron poles were the permanent points of the measurements. They were adjusted to provide a
227 horizontal support for the aluminium bar before measurements. Vertical holes were drilled in
228 the centre of the aluminium bar every 10 cm resulting in a total of 13 regularly spaced holes
229 (Fig. S1). To take the erosion measurements, a graduated rod was introduced in each of the
230 holes. The scale of the graduated rods allowed a direct measurement of the space between the
231 aluminium bar and the ground. An increase in space between measurements indicates erosion
232 whereas a decrease suggests an accumulation of soil. Measurements were taken in June 2019,
233 October 2019, June 2020 and September 2020, in order to assess the effect of restoration
234 treatments on soil erosion.

235

236 *2.5. Data analysis*

237 We used plant abundance, cover and richness of the entire plant community and of
238 transferred species to run statistical tests and to calculate restoration indices. Major soil and
239 microclimatic variables of restoration sites and potential reference sites were fitted to
240 multivariate models (NMDS) to identify the best references of each restoration site. The
241 identification was based on dissimilarity coefficients using Euclidean distances and is detailed
242 in Durbecq et al., (2020). We compared restoration sites and these best reference sites using
243 the restoration indices CSII_{norm} (normalized Community Structure Integrity Index) and HAI
244 (Higher Abundance Index). The CSII allows measuring which proportion of the species
245 abundance of the reference communities is represented in the restored communities, and the
246 HAI evaluates the proportions of the species abundance in the restored communities that are
247 higher than in the reference communities (Jaunatre et al., 2013).

248 We ran linear and generalized mixed models with transfer treatments as fixed effect
249 and site as random effect to analyse response variables (including restoration indices) to the
250 restoration treatments. In the analyses of plant abundance, quadrat within treatment was
251 additionally included as a random effect. Plant cover, species richness and restoration indices
252 were normally distributed and thus analysed using a Gaussian distribution with identity link.
253 Plant abundance was fitted using a Poisson distribution with log-link function. In the case of a
254 significant treatment effect, pairwise comparisons were used to compare differences between
255 transfer techniques (glht function in multcomp package; [Hothorn et al., 2008](#)).

256 A NMDS (Non-Metric Multidimensional Scaling) based on Bray–Curtis similarity was
257 applied to compare plant species composition of the five restoration sites and their best
258 reference sites. A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to
259 analyse whether the community composition was significantly different between treatments
260 (R package “vegan”). All analyses were performed using R 3.5.3 ([R Core Team 2019](#)).

261

262

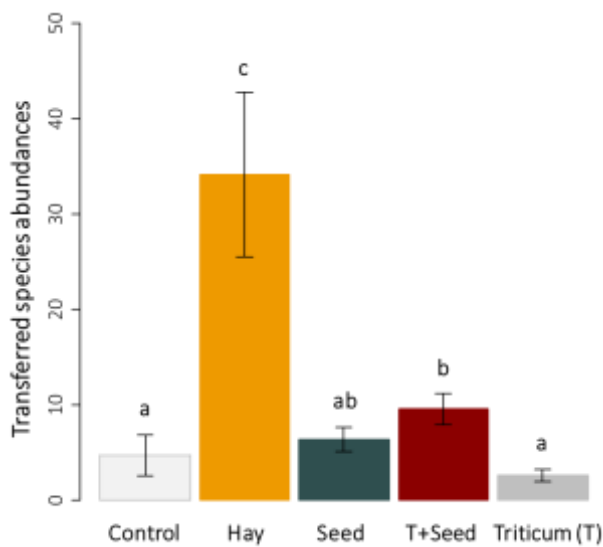
263 3. Results

264 The greenhouse tests revealed a mean density of 197.4 viable seeds/g in the brush harvest
265 material and 2.4 viable seeds/g in the hay. This corresponds to a comparable density of 1283
266 viable seeds per m² and 1200 viable seeds per m² transferred with brush material and hay to
267 the restoration sites, respectively.

268

269 *3.1. Effects of transfer techniques and wheat sowing on target species establishment*

270 Seedling emergence of transferred species was only 50/m² (without wheat) to 65/m² (with
271 wheat) in the brush material transfer and 200/m² in the hay transfer corresponding to 4 %, 5
272 %, and 17 % of the number of transferred viable seeds, respectively. Transferred species
273 abundance was significantly different between the restoration treatments ($\chi^2 = 51.85$, $df = 4$, P
274 < 0.001 ; Fig. 1). We found the clearly highest density of transferred species in the 'Hay'
275 treatment although seed density was similar to brush material according to germination tests.
276 The 'Seed' treatment involving brush material transfer without wheat addition was neither
277 significantly different to the control nor to the 'Triticum' treatment. Transferred seedling
278 abundance in the combined 'Triticum + Seed' treatment was significantly higher than in the
279 control but lower than in the 'Hay' treatment.



280

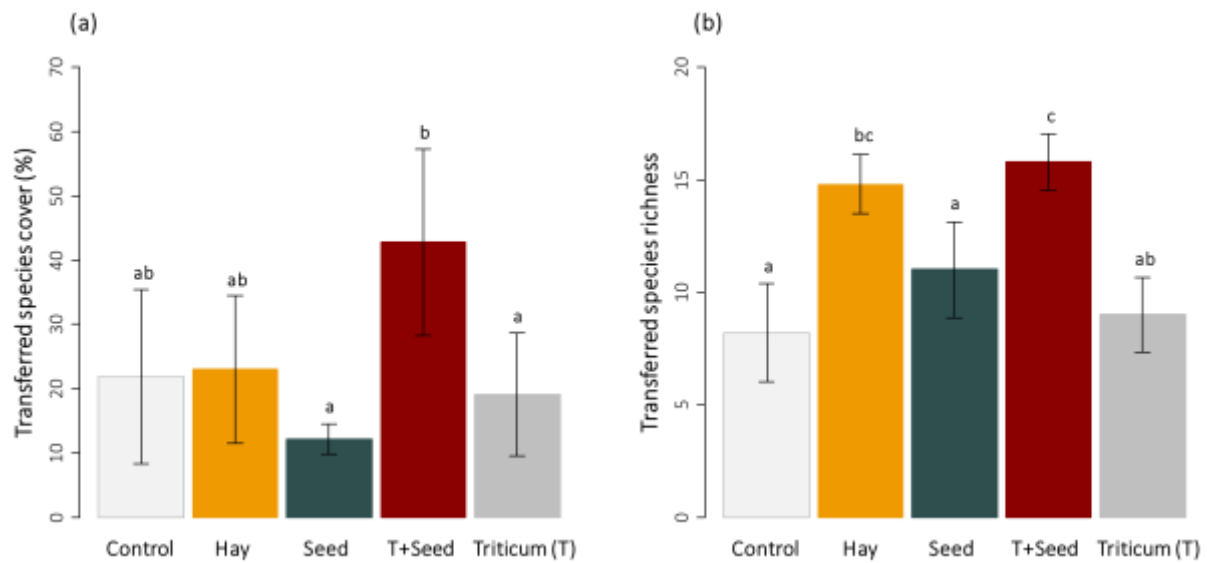
281 **Fig. 1.** Effect of seed transfer techniques on the abundance of transferred species estimated in
282 quadrats of 40 × 40 cm in 2019. Error bars represent ±SE and different letters indicate
283 significant differences between treatments ($P < 0.05$).

284

285 The treatments also had a significant effect on the second-year cover of transferred
286 species ($\chi^2 = 16.28$, $df = 4$, $P = 0.002$; Fig 2.a). However, the strongly positive effect of the 'Hay'
287 treatment vanished and the difference to the control was not significant any more. Transferred
288 species cover was significantly higher in the combined 'Triticum + Seed' treatment than in the
289 'Seed' and 'Triticum' treatments whereas all other treatments were not significantly different.

290 Similarly to transferred species cover (Fig. 2.a), richness of transferred species varied
291 significantly between treatments ($\chi^2 = 19.65$, $df = 4$, $P < 0.001$; Fig. 2.b). The 'Seed' treatment
292 was again only significantly different from the control if combined with wheat sowing ('Triticum
293 + Seed'). Contrary to transferred species cover but in line with first-year abundance, species
294 richness was significantly higher in the 'Hay' treatment than in the control. The 'Hay' and the
295 combined 'Triticum + Seed' treatments comprised on average seven more transferred species
296 (± 3 species) than the control. The 'Seed' treatment without wheat sowing was not significantly
297 different from the control or the 'Triticum' treatment. Similar treatment effects were visible for
298 the total species richness (Fig. S2). However, only the difference between the combined
299 'Triticum + Seed' treatment and the control was significant.

300



301

302 **Fig. 2.** Effect of seed transfer techniques on **(a)** transferred species cover, and **(b)** transferred
 303 species richness, both based on 2020 cover values and estimated in quadrats of 2 × 2 m. Error
 304 bars represent ±SE and different letters indicate significant differences between treatments (P
 305 < 0.05).

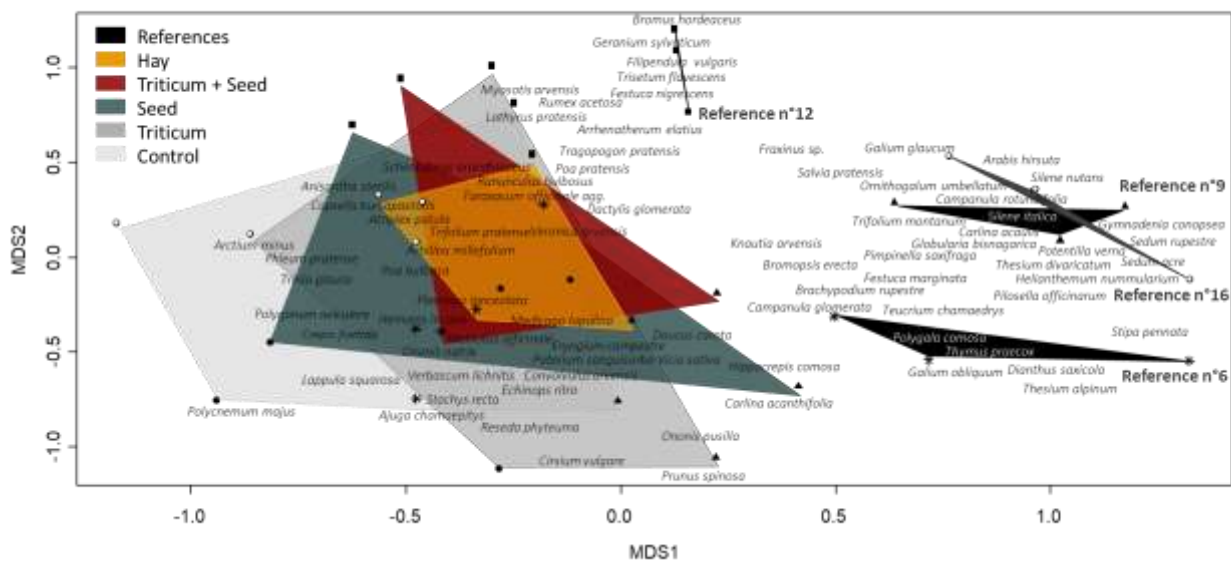
306

307 **3.2. Comparison with best references of each restoration site**

308 The plant species composition of the restoration sites was very different from that of
 309 reference sites in all treatments (Fig. 3). Restoration and reference sites were particularly
 310 separated on the first axis. This axis represented a disturbance gradient with annual and ruderal
 311 species occurring on the left together with restoration sites (*Arctium minus* (Hill) Bernh.,
 312 *Polygonum aviculare* L., *Anisantha sterilis* (L.) Nevski, etc.) and perennial grassland species on
 313 the right together with reference sites (*Stipa pennata* L., *Helianthemum nummularium* (L.) Mill.,
 314 *Pilosella officinarum* F.W.Schultz & Sch.Bip., etc.) . The differences between reference sites
 315 reflect the heterogeneity of plant communities according to different environmental conditions
 316 that are independent of degradation. They were particularly separated on the second NMDS

317 axis representing a productivity gradient from stony, xeric sites in the lower part of the biplot
 318 to more humid, mesophilic sites in the upper part. There was a large overlap between the five
 319 treatments within restoration sites, but the treatment effect was still significant ($F = 1.432$, df
 320 $= 4$, $P = 0.012$). As expected, the unsown control showed the greatest distance to the
 321 references. The 'Hay' and 'Triticum + Seed' treatments were closest to the reference sites,
 322 followed by the 'Seed' treatment without wheat. However, the latter treatment was not much
 323 closer to the reference communities than wheat sowing alone. The 'Triticum' treatment
 324 showed the highest variation between sites resulting in a large NMDS polygon.

325



326

327 **Fig. 3.** NMDS of plant species composition in the five transfer technique treatments compared
 328 to plant species composition in the best reference for each restoration site previously identified
 329 in Durbecq et al., (2020). Polygons indicate the position of the outmost plots in each treatment
 330 (stress = 0.20). Different symbols indicate the five different restoration sites and corresponding

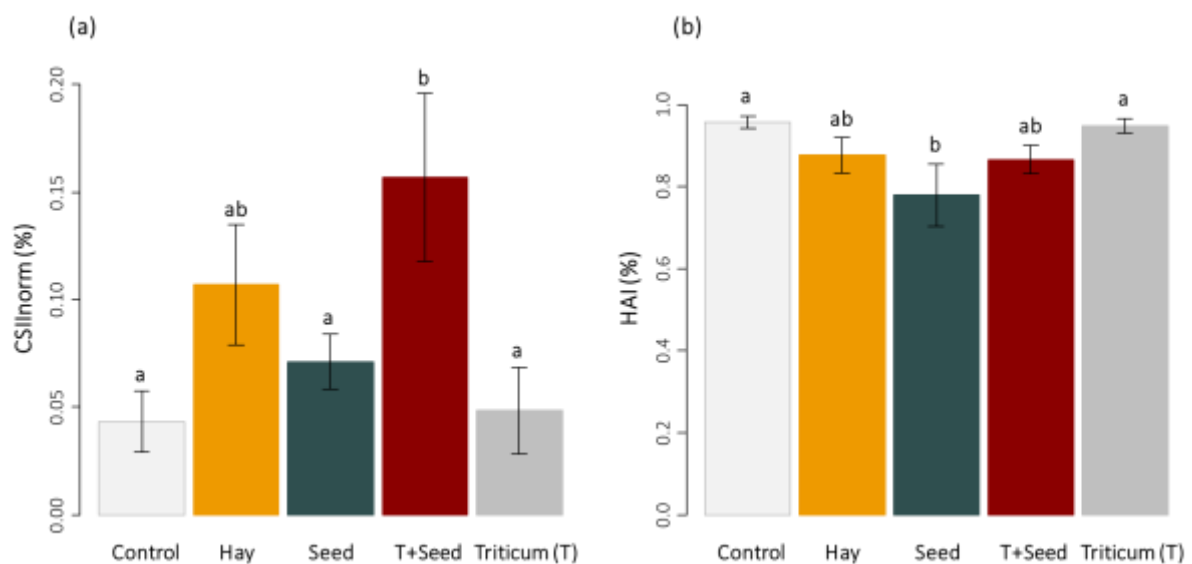
331 references: ● and ○ for sites corresponding to reference n°16 (same reference for the two
332 restoration sites), ■ to reference n°12, * to reference n°6, and ▲ to reference n°9.

333

334 The CSII_{norm} calculated for each restoration site compared with their respective best
335 reference showed a significant difference between treatments ($\chi^2 = 18.02$, $df = 4$, $P < 0.01$; Fig.
336 4.a and 5). CSII_{norm} was significantly higher in the combined 'Triticum + Seed' treatment than in
337 the control, the 'Triticum' and the 'Seed' treatments. The 'Hay' treatment was not significantly
338 different from other treatments.

339 The HAI was also significantly different between treatments ($\chi^2 = 11.44$, $df = 4$, $P < 0.05$,
340 Fig. 4.b and 5). The lowest HAI was found in the 'Seed' treatment being significantly lower than
341 the control and the 'Triticum' treatment, indicating significantly lower non-target abundances
342 in the 'Seed' treatment. Differences between other treatments were not significant.

343



344

345 **Fig. 4. (a)** CSII_{norm} and **(b)** HAI, comparing the plant communities of transfer technique
346 treatments of each restoration site with their respective best reference site. Error bars

347 represent \pm SE and different letters indicate significant differences between treatments ($P <$
348 0.05).

349

350 The significant differences in $CSII_{norm}$ were explained by a higher number of target
351 species in the 'Hay' and in the combined 'Triticum + Seed' treatments compared to the other
352 treatments. Target species were those occurring in the best references such as *Plantago media*
353 L., *Festuca cinerea* Vill., *Teucrium chamaedrys* L., *Poa pratensis* L., *Hippocrepis comosa* L., *Lotus*
354 *corniculatus* L., *Silene vulgaris* (Moench) Garcke, *Eryngium campestre* L., *Poterium sanguisorba*
355 L. and *Trifolium pratense* L. (Fig. 5). In the 'Hay' and the 'Triticum + Seed' treatments, the cover
356 of several target species was even higher than in the references, (e.g. *Poterium sanguisorba* L.,
357 *Medicago lupulina* L., *Trifolium repens* L., *Trifolium pratense* L., *Convolvulus arvensis* L.).

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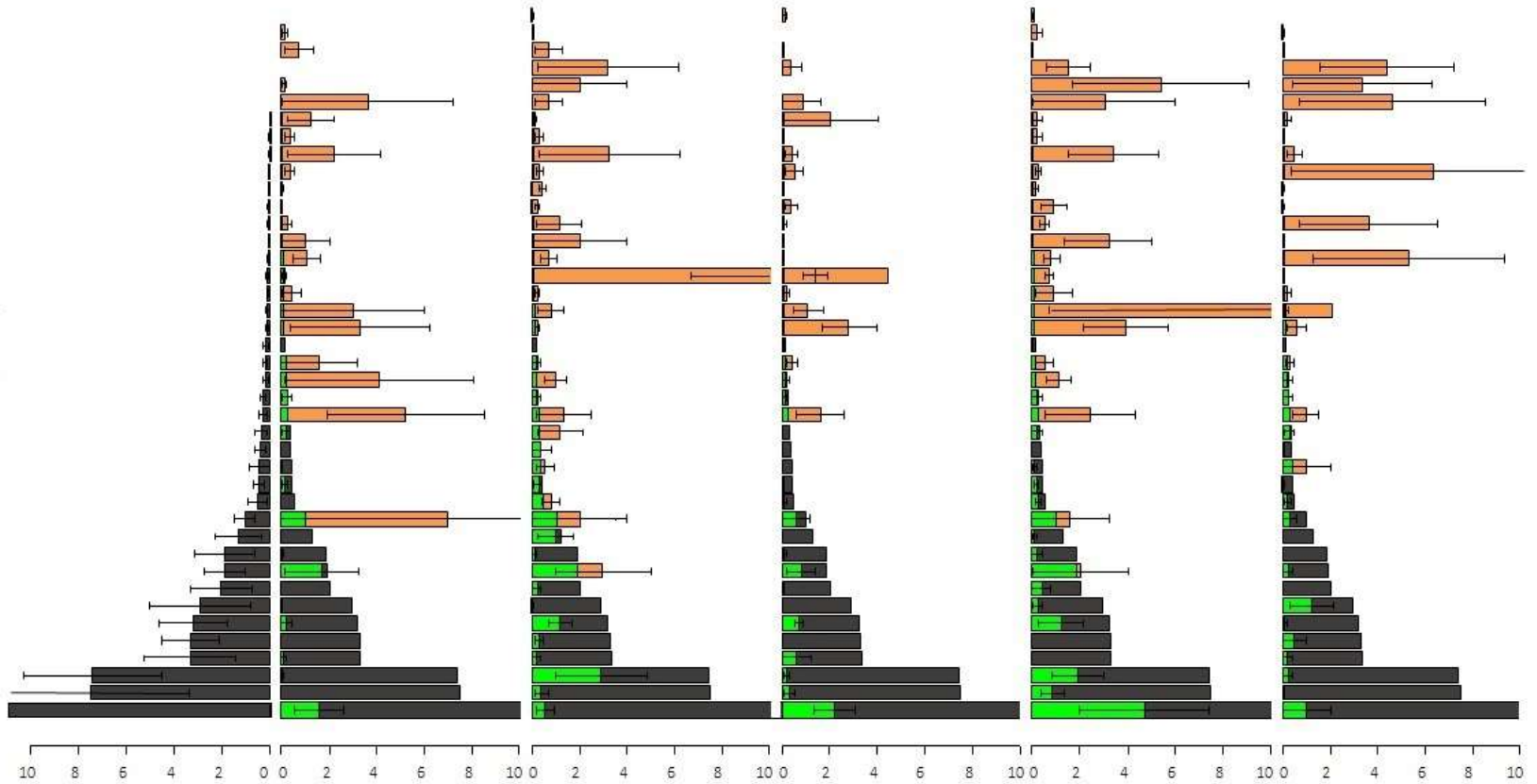
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366

- Alyssum alyssoides* *
- Stachys recta* *
- Potentilla reptans* *
- Convolvulus arvensis*
- Melilotus officinale*
- Lappula squarosa*
- Polygonum aviculare*
- Echinops ritro*
- Trifolium pratense* *
- Lactuca serriola*
- Veronica arvensis*
- Onobrychis vicifolia* *
- Arenaria serpyllifolia* *
- Trifolium repens*
- Medicago lupulina*
- Galium mollugo* agg.
- Ranunculus bulbosus* *
- Schedonorus arundinaceus* *
- Plantago lanceolata* *
- Pimpinella saxifraga* *
- Taraxacum officinale* agg. *
- Poterium sanguisorba*
- Daucus carota*
- Achillea millefolium* *
- Eryngium campestre*
- Tragopogon pratensis*
- Silene vulgaris* *
- Lotus corniculatus* *
- Galium verum*
- Hippocrepis comosa*
- Knautia arvensis* *
- Festuca marginata* *
- Poa pratensis* *
- Teucrium chamaedrys*
- Festuca cinerea*
- Dactylis glomerata* *
- Salvia pratensis* *
- Anthyllis vulneraria*
- Plantago media* *
- Rhinanthus alectorolophus* *
- Bromopsis erecta* *



367

Species

Reference

Control

Hay

Seed

Triticum + Seed

Triticum

368

369

370 Fig. 5. Mean target plant cover of abundant species (> 9 samples, 41 of 259 species in total) in
371 restoration treatments and the best reference community. Different colours represent the
372 mean cover proportion in references (*black*), the mean cover proportion in communities under
373 restoration up to the mean cover in the reference communities (*green*), and the mean cover
374 proportion exceeding that of the reference communities (*orange*). *Asterisks* indicate
375 transferred species. For readability, the x-axis is limited to 10 % cover (only *Bromopsis erecta*
376 (Huds.) Fourr., *Schedonorus arundinaceus* (Schreb.) Dumort. and *Galium molugo* agg.
377 exceeded).

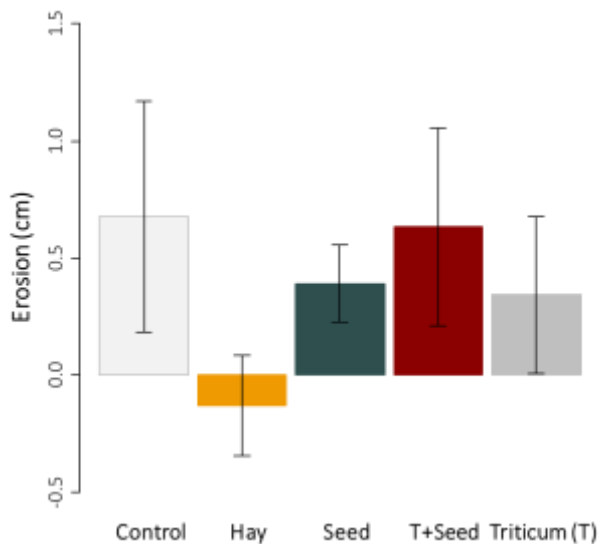
378

379

380 ***3.3. Ecosystem function: erosion control***

381 Erosion monitoring did not show significant treatment effects at the end of the observation
382 period. Lowest erosion was observed in the 'Hay' treatment but due to high between-site
383 variation the difference to other treatments was not significant (Fig. 6). Intermediate
384 measurements demonstrated a high temporal variability of erosion and of treatment effects
385 on erosion (Fig. S3).

386



387

388 **Fig.6.** Effect of seed transfer techniques on soil erosion. Error bars represent \pm SE. Positive
 389 values show higher erosion, thus a lesser amount of material on the ground 14 months after
 390 the beginning of the experiment.

391

392

393 4. Discussion

394 Both techniques, brush-harvested propagule transfer and hay transfer, allowed the
 395 introduction of high numbers of viable seeds. However, first-year seedling recruitment was
 396 much higher in hay transfer than in brush material transfer. Additional wheat sowing had a
 397 particularly positive effect on seedling establishment from brush material resulting in a second-
 398 year cover of transferred species similar to that of hay. Brush material transfer alone did neither
 399 increase transferred species cover nor plant species richness. According to transferred species
 400 abundance and cover, hay transfer and brush material transfer combined with wheat sowing
 401 were also most successful in restoring the plant species composition of the reference. Soil
 402 erosion was not affected by any restoration treatments.

403

404 *4.1. Effect of seed-addition techniques on transferred species recruitment*

405 Brush harvesting has many technical advantages compared to hay cutting allowing selection
406 and cleaning of seeds, drying and particularly easy storage (lower volume than hay) under
407 optimum temperature and humidity (Edwards et al., 2007; Vitis et al., 2020; Frischie et al.,
408 2020). Contrary to hay cutting, it is possible to brush-harvest several times a season thus
409 maximizing the number of transferred species (Edwards et al., 2007; Scotton & Ševčíková,
410 2017). The possibility to use grasslands for hay making after brush harvesting is another
411 advantage reducing losses for livestock farmers. However, several studies obtained a low
412 efficiency in plant establishment from brush material compared to hay transfer (Edwards et al.,
413 2007; Sengl et al., 2017; Albert et al., 2019). Albert et al., (2019) explained the lower seed
414 number per harvested area by the higher working height of brushes compared to mowing
415 machinery missing the seeds of low-growing species.

416 In our study, the brush material contained as many viable seeds as the hay suggesting that
417 the low recruitment compared to hay transfer was due to lower germination and seedling
418 survival. The mulch layer resulting from hay transfer may improve seedling recruitment of
419 transferred species through an increase in soil moisture retention (Donath et al., 2007; Mollard
420 et al., 2014; Havrilla et al., 2020). Soil moisture retention and temperature buffering are
421 important factors influencing germination in our study region characterized by shallow soils,
422 spring frosts and high solar radiation. Furthermore, hay mulch protects seeds from predation,
423 and animal trampling (Scotton et al., 2012; Vanderburg et al., 2020) and limits competition of
424 ruderal species in early stages of grassland restoration (Kiehl & Wagner, 2006). Additionally, a
425 hay layer may reduce surface runoff (Graiss & Krautzer, 2011) and improve seed adherence to

426 the soil (Chambers, 2000; Havrilla et al., 2020). High recruitment in the hay transfer treatment
427 suggests that such positive effects prevailed in our study over negative effects of a mulch layer
428 on transferred species establishment, such as light limitation (Eckstein & Donath, 2005). Such
429 mulch effects are highly species-specific (Sonkoly et al., 2020), and in our study the mulch layer
430 had most likely an indirect positive effect on target species by having a direct negative effect
431 on ruderal species. Furthermore, a mulch layer may stronger limit light availability of seeds in
432 the soil (spontaneous, mostly ruderal species) than of seeds of transferred species that remain
433 at the soil surface or even in upper mulch layers.

434 Effects of temporary wheat cover on seedling recruitment may be similar to hay mulch
435 effects, such as protection against drought and solar radiation (Wright et al., 2014).
436 Additionally, belowground effects may facilitate seedling recruitment and establishment since
437 wheat roots stabilize the soil and foster the recolonization of the soil fauna (Faivre 2000). In
438 modifying soil structure and composition (Pohl et al., 2009; Liu et al., 2018), wheat can be
439 considered as a nurse crop (Padilla et al., 2006). Many high-altitude restoration studies aimed
440 at improving recruitment conditions and reducing soil erosion using nurse species or wheat
441 straw addition to stabilize the soil (Graiss & Krautzer, 2011; Kavian et al., 2018; Scotton, 2019).
442 However, propagule run-off, germination and early survival are less likely affected by wheat
443 sowing than by hay mulch since wheat cover develops later. In our study, this was probably the
444 reason for an absence of a wheat sowing effect on first-year abundance of species transferred
445 with brush material whereas the effect on second-year cover was strongly positive. Like hay
446 transfer, facilitative effects of wheat sowing prevailed over negative effects of competition for
447 light and water observed in other studies on additional sowing (Donath et al., 2006; Wright et
448 al., 2014).

449 Soil preparation before sowing has often been recommended to improve seedling
450 recruitment in sowing of brush-harvested seeds or seed mixtures (Kiehl et al., 2010; Edwards
451 et al., 2007; Klaus et al., 2017; Shaw et al., 2020). Similarly to hay mulch, soil preparation
452 increases seed and water retention as well as seed adhesion (Chambers, 2000) and may thus
453 compensate for the absence of a hay mulch layer limiting seed run-off. In our study area, a
454 previous experiment testing soil preparation effects on seedling recruitment showed a strong
455 increase in first-year abundance of transferred species (Durbecq et al., 2021). Thus, the plots
456 that received brush material in our study may particularly benefit from previous soil tillage and
457 a combination with additional wheat sowing may be the optimum strategy for seedling
458 recruitment and establishment.

459

460 ***4.2. Successful restoration of reference communities and erosion protection***

461 Seed addition using brush material and hay of the donor site was successful in increasing the
462 similarity to best references at plant community level. As in the analysis of cover and number
463 of species transferred from the donor site, best restoration results were obtained for hay
464 transfer and the combination of brush material with wheat sowing, showing highest similarity
465 to references in plant species composition and highest target abundance (higher $CSII_{norm}$ =
466 abundance of species occurring in the reference). This finding confirmed that a dead (hay) or
467 living (wheat) “nurse cover” improves seedling establishment of target (reference
468 communities) and transferred (donor community) species (Graiss & Krautzer, 2011; Kavian et
469 al., 2018; Scotton, 2019). The brush material transfer without wheat sowing did not increase
470 similarity to references nor target abundance. However, HAI (proportion of non-target
471 abundances) of this treatment was lower compared to the control whereas the HAI of brush

472 material with wheat and hay transfer were not significantly different from the control. These
473 results indicated that hay mulch and wheat cover did not only provide better conditions for
474 target species but also for non-target species recruitment.

475 In mountain and alpine grasslands with more or less steep slopes, soil stabilization
476 processes are slow, which increases soil erosion (Wiesmair et al., 2017). Erosion control is thus
477 essential to restore these ecosystems (Pohl et al., 2009; Scotton, 2019; Löbmann et al., 2020).
478 Without plant cover, erosion, depletion of organic matter and gully formation may compromise
479 restoration approaches (Dupin et al., 2019). Several authors have shown a negative linear
480 relationship between vegetation cover and soil runoff (Peratoner, 2003; Liu et al., 2018; Gu et
481 al., 2020). Hence, immediate revegetation by locally adapted propagules is widely
482 recommended (Scotton et al., 2009; Wiesmair et al., 2017; Dupin et al., 2019). Using well-
483 adapted temporary nurse crop may have a stronger positive effect on soil erosion control than
484 dead plant material, such as hay or straw, since developing roots allow a belowground
485 stabilisation of the soil (Pohl et al., 2009). According to Liu et al., (2018) and Gu et al. (2020), an
486 average total vegetation cover of 60 % observed in our study may reduce soil erosion by up to
487 80 % compared to bare soil. However, our restoration treatments did not sufficiently influence
488 total plant cover compared to control and thus the treatment effect on soil erosion was not
489 significant. Run-off at several places may have been compensated by sediment accumulation
490 in others without changing the overall erosion measurement. To analyse erosion and sediment
491 accumulation within plots in detail combined sediment-runoff collection systems may be used
492 with water collection and storage tanks being placed at the down slope side (Parsons et al.,
493 2006; Phan Ha et al., 2012).

494 Contrary to our results, Kavian et al. (2018) found a long-term reduction in soil runoff using
495 wheat residual as agriculture mulch. Our restoration sites were not characterized by steep
496 slopes, thus limiting soil run-off and the probability to find differences between treatments.
497 Additionally, spontaneous vegetation emerging from the soil seed bank dominated in the
498 beginning limiting the treatment effect.

499

500 5. Conclusions

501 All applied transfer techniques were successful in establishing plant species of the donor
502 community. However, the transfer of brush harvested seed material was only efficient together
503 with wheat sowing. Our results demonstrated that restoration of grasslands of the mountain
504 altitudinal belt with shallow and stony soils clearly benefit from dead (hay) or living (wheat)
505 vegetation cover providing a nurse effect. Facilitation effects prevail over competition and/or
506 reduction in resources such as light (Eckstein & Donath, 2005; Padilla et al., 2006; Wright et al.,
507 2014). Hay transfer was the best method to increase germination and seedling recruitment but
508 the difference to brush material transfer with wheat sowing vanished in the second year
509 indicating higher seedling mortality in the hay mulch (Eckstein & Donath, 2005). The lower
510 seedling recruitment in brush material transfer may be compensated by harrowing the soil
511 before brush material transfer to improve recruitment conditions (Kiehl et al., 2010; Klaus et
512 al., 2017; Durbecq et al., 2021). Propagule transfer did not improve the soil erosion control.
513 Short-lived species spontaneously emerging from the soil seed bank dominated in the
514 beginning reducing the magnitude of treatment effects. Long-term monitoring is required to
515 evaluate the replacement of short-lived ruderals by the transferred perennial species often
516 observed in restoration studies (Albert et al., 2019; Kiss et al., 2020; Shaw et al., 2020).

517

518

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523

524 **Declaration of competing interest**

525 The authors declare that they have no competing interests.

526

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532

533 **Appendix 1. Supplementary material**

534

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542

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