1 **Can the response of above- and below-ground traits to overgrazing vary between**
2 **annual and perennial species?**

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12 **Running Head:** Above- and below-ground traits in response to overgrazing.

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16

17 **Abstract**

18 Understanding functional traits that capture species response to grazing is crucial for
 19 uncovering mechanisms underlying the grazing-induced alterations in vegetation
 20 composition. Currently, the majority of studies ignore the effects of life form on the
 21 response of above- and below-ground traits to grazing. In this study we quantified i)
 22 whether below-ground traits exhibit similar response to overgrazing as do
 23 above-ground traits; and ii) whether the response of above- and below-ground traits to
 24 overgrazing varied with life form (annual versus perennial species). To testify the
 25 generality of these two questions, we compared common grassland species between
 26 an undisturbed and an over grazed meadow at each of four elevations ranging from
 27 3000m to 3600m on the Qinghai Tibetan Plateau. We found both above-ground and
 28 below-ground traits exhibited similar resource conservation *vs.* resource acquisition
 29 trade-off for responding to overgrazing. Moreover, perennial species but not annual
 30 species determine the response of above- and below-ground traits to overgrazing. This
 31 work bridges the gap in the literature for the influence of land-use (in the absence and
 32 presence of overgrazing) and life forms (annual and perennial species) on
 33 species-specific response at both above-, and below-ground level.

34 **Key-words:** above-ground and below-ground traits, land use, life form, resource
 35 conservation *vs.* resource acquisition trade-off, restoration.

36 **Introduction**

37 Grazing is one among the most significant drivers of global vegetation composition
 38 (Díaz *et al.*, 2007; Stein *et al.*, 2016). Understanding functional traits that capture
 39 species response to grazing is crucial for uncovering mechanisms underlying the
 40 grazing-induced alterations in vegetation composition (Díaz *et al.*, 2001; Cingolani *et*
 41 *al.*, 2005; de Bello *et al.*, 2005; Díaz *et al.*, 2007; Ewu *et al.*, 2009; Golodets *et al.*,
 42 2010). Generally, above-ground traits such as shorter plant height and higher specific
 43 leaf area (SLA) can help the plants have high resource acquisition for tolerating high
 44 grazing pressure (Díaz *et al.*, 2001; Li *et al.*, 2017). In contrast, in the undisturbed
 45 condition, species prefer to have lower SLA but higher plant heights, which is
 46 regarded as a strategy for high resource conservation to adapt to resource limitation
 47 (Westoby, 1999).

48 It has also been found that below-ground traits play a key role in mediating
 49 grazing-induced alterations to vegetation composition (Klump *et al.*, 2009; McInenly
 50 *et al.*, 2010). However, due to the notable lack of relevant below-ground trait data
 51 (Bergmann *et al.*, 2017), it remains unclear whether below-ground traits exhibit
 52 similar high resource acquisition (e.g., higher RD, SRL, SRA, but lower RTD) for
 53 tolerating grazing as do above-ground traits (Craine *et al.*, 2001; Hodge, 2004;
 54 Klump *et al.*, 2009; McInenly *et al.*, 2010; Roumet *et al.*, 2016; Kramer *et al.*, 2016;
 55 Feng *et al.*, 2018). This limits our understanding of how livestock influence
 56 vegetation compositions (Li *et al.*, 2017).

57 Determining the response of above-ground and below-ground traits against

58 grazing requires an understanding of how grazing influences species composition
 59 (Díaz *et al.*, 2001; James *et al.*, 2001). A global meta-analysis showed that
 60 overgrazing promotes annual species over perennial species (Díaz *et al.*, 2007).
 61 Conversely, without grazing pressure, perennial species are expected to dominate
 62 (Zhang *et al.*, 2018). This is likely due to the fact that annual species tend to have
 63 above- and below-ground traits that are associated with high resource acquisition,
 64 whereas perennial species tend to possess traits related to a resource conservation
 65 strategy (Roumet *et al.*, 2006, 2016; Zhang *et al.*, 2018). As a result, the response of
 66 above-ground and below-ground traits to overgrazing may vary between annual and
 67 perennial species. However, the effect of life form (annual versus perennial species)
 68 on overgrazing induced alterations to above- and below-ground traits have been
 69 hardly considered.

70 Here, our goal was to test i) whether above-, and below-ground traits have
 71 similar response to overgrazing; and ii) whether the response of above-, and
 72 below-ground traits to overgrazing differs between annual and perennial species. To
 73 testify the generality of these two goals, we compared above-, and below-ground traits
 74 for all common species found in one undisturbed meadow and one overgrazed
 75 meadow at each of four elevations ranging from 3000 to 3600 m in Qinghai Tibetan
 76 plateau. We hypothesized that 1) both above-, and below-ground traits exhibited a
 77 resource conservation *vs.* resource acquisition trade-off for responding to overgrazing;
 78 and 2) the response of above- and below-ground traits to overgrazing varies between
 79 annual and perennial species.

80 **Methods and materials**

81 **Study site**

82 The maximum carrying capacity for cold season is approximately 2 yaks per hectare
 83 on Qinghai-Tibetan Plateau (Dong *et al.*, 2015). In light of this standard, four
 84 overgrazed meadows that have undergone overgrazing at a comparable intensity (e.g.,
 85 overgrazed by approximately the same number of yaks (approximately 4 yaks per
 86 hectare) in cold season every year) for nearly 30 years along an increasing elevation
 87 ranging from 3000 to 3600 m above mean sea level in the eastern part of the
 88 Qinghai-Tibetan Plateau, distributed in Hezuo city, Gansu province, China (34°55'N,
 89 102°53'E; 3000 a.s.l.), Ruergai County, Sichuan province, China (34°1'N, 102°43'E;
 90 3200a.s.l.) and Maqu County, Gansu province, China (34°5'N, 102°10'E; 3400 and
 91 3600a.s.l.). At each elevation, we also sampled one undisturbed meadow for
 92 comparison. All sampling regions are characterized by a cold and dry climate; with a
 93 mean annual temperature of 2.4 to 3.2 °C. Mean annual precipitation of 530 to 560
 94 mm is primarily distributed from July to August. The local vegetation in undisturbed
 95 sites is dominated by herbaceous species, such as *Elymus nutans* (Griseb), *Kobresia*
 96 *pygmaea* (C. B. Clarke), and *Thermopsis lanceolata* (R. Br) (Zhang *et al.*, 2015).
 97 Soils are classified as alpine meadow soils (Zhang *et al.*, 2018).

98 **Field sampling**

99 Sampling was conducted in August, during the peak of the growing season in 2017. At
 100 each of the four elevations, thirty $0.5 \times 0.5 \text{ m}^2$ plots were arranged along four parallel
 101 transects in the fenced area and the adjacent overgrazed area of one meadow, with a

102 20 m spacing between the closest edges of the two areas. The plots were spaced at 20
103 m intervals. For each of the 30 plots, species compositions was recorded.

104 ***Plant above-ground and root traits measurements***

105 All common species sharing between undisturbed and grazed meadows were sampled
106 to measure three above-ground traits, leaf photosynthesis rate (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$),
107 specific leaf area (SLA; cm^2/g) and above-ground maximum height (H ; m). Further,
108 five root traits, root average diameter (RD; cm), root biomass (RB; g), specific root
109 length (SRL; cm/g), root tissue density (RTD; g/m^{-3}), specific root area (SRA; cm^2/g)
110 were recorded. All of these traits could be good predictors of resource acquisition vs.
111 resource conservation trade-off (Díaz *et al.*, 2001; Roumet *et al.*, 2006). Traits were
112 measured from three to five mature individuals per species and detail measurement
113 was described in Bergmann *et al.* (2017) and Zhang *et al.* (2018) and Supplementary
114 materials.

115 **Statistical methods**

116 First, we tested whether there were differences in the above- and below-ground traits
117 for all common species shared between undisturbed and overgrazed meadows at all
118 four elevations using a Wilcoxon signed-rank test. Next, a Spearman correlation test
119 was used to examine the bivariate relationships among all above- and below-ground
120 plant traits at all elevations. Finally, a principal component analysis (PCA) was
121 employed to evaluate which of the eight above-ground and root traits play an
122 important role in affecting species distributions between undisturbed and overgrazed
123 meadows at all elevations. Given the unique set of traits between annual and perennial

124 plant species (Roumet *et al.*, 2006; Zhang *et al.*, 2018), the above analyses were also
125 performed separately for annuals and perennials to understand whether the response
126 of above- and below-ground traits to overgrazing vary between annual and perennial
127 species.

128 **Results**

129 In total, we sampled 53-77 species in the undisturbed meadows from 3000 to
130 3600m elevation, of which 12-22 were annuals and 41-55 were perennial species. On
131 the other hand, only 40-51 species, 22-24 annual and 18-27 perennials, could be
132 identified in the sampling of the overgrazed meadow (Table S1). However, species
133 composition was similar between the undisturbed and overgrazed meadows as the two
134 meadows shared 22-42 species (12-15 annual and 10-27 perennial species) in
135 common (Table S1).

136 The Wilcoxon signed-rank test showed that all shared species had significantly
137 lower root biomass (RB), root tissue density (RTD), and above-ground maximum
138 height (H) in the overgrazed meadows than those in the undisturbed meadows at all
139 four elevations. In contrast, overgrazed meadows had higher root average diameter
140 (RD), specific root length (SRL), specific root area (SRA), leaf photosynthesis rate (A)
141 and specific leaf area (SLA) than those in the undisturbed meadow (Fig. 1).
142 Consistent results could still be observed in perennial species, when we performed
143 Wilcoxon signed-rank test separately for annuals and perennials (Fig. 1). However,
144 for annual species, there are not any differences in all above-ground and
145 below-ground traits between undisturbed and overgrazed meadows (Fig. 1).

146 We observed strong correlations amongst the five root traits, as well as between
147 the three above-ground traits, for all common species in both, undisturbed and grazed
148 meadows at all four elevations (Fig. 2). However, when we tested these correlations
149 separately for annuals and perennials, consistent results could still be observed in
150 perennial species in both undisturbed and overgrazed meadows at all elevations (Fig.
151 2). However, for annual species, most of these strong correlations were
152 non-significant in both undisturbed and overgrazed meadow at all elevations (Fig. 2).

153 PCA results revealed that undisturbed and overgrazed species were significantly
154 separated along axis 1 at all elevations. PCA axis 1 had a strong positive loading for
155 SRL, SRA, A and SLA for all common species at all elevations, but negative loading
156 for RD, RB, RTD and H (Fig. 3 and Tables S2). PCA axis 2 was significantly
157 positively associated with RB and RTD (Fig. 3, and Table S2). When performing PCA
158 separately for annual and perennial species, we still found consistent PCA results for
159 perennial species. However, we found different PCA results for annual species,
160 because undisturbed and overgrazed species could not be significantly separated along
161 axis 1 and axis 2 at all elevations (Fig. S1 and Table S2). Moreover loading for traits
162 that was significantly associated with PCA axis 1 and 2 were different among all
163 elevations (Fig. S1 and Table S2).

164 **Discussion**

165 In this study, we quantified how overgrazing affect above-ground and
166 below-ground traits; and whether the response of above- and below-ground traits to
167 overgrazing varied with life form (annual versus perennial species). As we

168 hypothesized, both above-ground and below-ground traits exhibited a resource
169 acquisition vs. resource conservation trade-off for responding to overgrazing. The
170 response of above- and below-ground traits to overgrazing differed between annual
171 and perennial species, with perennial species determining the response of above- and
172 below-ground traits to overgrazing.

173 **The response of above-ground and below-ground traits to overgrazing for all**
174 **species at all elevations**

175 A shift from resource conservation to resource acquisition at above-ground level have
176 been widely found to tolerate grazing, which force species to have higher SLA,
177 photosynthesis rate, but lower height after overgrazing than those in the undisturbed
178 condition (Díaz *et al.*, 2001; Spasojevic *et al.*, 2010; Laliberté and Tylianakis, 2012;
179 Li *et al.*, 2017). It has also been found that this resource conservation vs. resource
180 acquisition trade-off has also led to strong correlation among SLA, photosynthesis
181 rate and height (Wright *et al.*, 2004; Osnas *et al.*, 2013). Here we observed consistent
182 trait variations and correlation among SLA, photosynthesis rate and height for all
183 species in both undisturbed and overgrazed meadows at all four elevations. This
184 indicated that a trade-off between resource acquisition vs. resource conservation at
185 above-ground level likely determines plant tolerance to overgrazing in Qinghai
186 Tibetan plateau.

187 A number of studies have found that the trade-off between resource acquisition
188 vs. resource conservation can also be found in below-ground traits, similar to what
189 have been found in above-ground traits (Withington *et al.*, 2006; Mommer and

190 Weemstra, 2012; Reich, 2014; Roumet *et al.*, 2016). For example, resource
 191 acquisition may need species to have high SRL, SRA, but low RTD, RB and RD to
 192 possess fast-growing, whereas, resource conservation may force species to have high
 193 RTD, RB and RD, but low SRL and SRA (Reich, 2014; Roumet *et al.*, 2016).
 194 Likewise, this resource acquisition vs. resource conservation trade-off at
 195 below-ground level can also led to significant root correlations (Withington *et al.*,
 196 2006; Prieto *et al.*, 2015; de la Riva *et al.*, 2018). Indeed, we found consistent trait
 197 variations and correlations among below-ground traits (SRL, SRA, RTD, RD and RB)
 198 at all elevations. This, indicated below-ground traits have also a shift from resource
 199 conservation to resource acquisition to tolerate overgrazing as above-ground traits
 200 does.

201 In the undisturbed meadows, resource conservation can also force species to
 202 have low photosynthetic rates and SLA, which require conservative root structures
 203 (e.g., roots with high root tissue density, root diameter and biomass, and/or low
 204 specific root length and area) to ensure high overall conservation of resources
 205 (Eissenstat, 2002; Fort *et al.*, 2013). In contrast, in the grazed meadow, resource
 206 acquisition tends to make species possess high photosynthetic rates and SLA, which
 207 requires roots with high specific root length and area, and low root tissue density,
 208 diameter and biomass to ensure sufficient nutrient supply to achieve fast plant growth
 209 (Reich, 2014; de la Riva *et al.*, 2018). Thus, significant above-ground -below-ground
 210 traits relationship may be observed in both undisturbed and grazed meadows. Indeed,
 211 significant relationships between above- and below- ground traits have been observed

212 in multiple studies in undisturbed meadows (Wardel *et al.*, 2004; Liu *et al.*, 2010;
213 Valverde-Barrantes *et al.*, 2017; de la Riva *et al.*, 2018). However, nearly no study
214 reported strong relationships between above-ground traits and below-ground traits
215 after overgrazing. Here we observed consistently significant relationships between
216 above- and below- ground traits in both undisturbed and overgrazed meadows at all
217 elevations. Thus, above-ground traits might act as a proxy for below ground traits in
218 revealing the response to overgrazing at the below-ground level.

219 Principal component analysis revealed that undisturbed and overgrazed species
220 were significantly separated along axis 1, which was significantly positively
221 associated with SRL, SRA, A and SLA, but negatively related RD, RB, RTD and H.
222 Since high SRL, SRA, A and SLA represented high resource acquisition, whereas,
223 high RD, RB, RTD and H indicated high resource conservation (Wright *et al.*, 2004;
224 Reich, 2014; de la Riva *et al.*, 2018). Thus the shift from resource conservation to
225 resource acquisition determine species distribution between undisturbed and
226 overgrazed meadows.

227 **Different response of above-ground and below-ground traits to overgrazing** 228 **between annual and perennial species**

229 It has been universally found that grazing promotes annual over perennial
230 species in grassland ecosystems (Díaz *et al.*, 2007). Our study supports this trend
231 where we found that after overgrazing perennial species decrease 2-2.3 times, whereas,
232 annual species increase 1.2-1.9 times. Especially at 3600m elevation, after
233 overgrazing, annual species is more than perennial species. Annuals tend to have traits

234 associated with a higher resource acquisition strategy, while perennial species tend to
 235 have traits associated with a resource conservation strategy (Roumet *et al.*, 2006;
 236 Zhang *et al.*, 2018). As a result, the outcomes for trait variations, trait-trait
 237 correlations and PCA may vary between annual species and perennial species. Indeed,
 238 consistent trait variations, trait-trait correlations and PCA results for all species can
 239 merely be found in perennial species but not annual species at all elevations. Our data,
 240 on one hand indicated that the response of above- and below-ground traits to
 241 overgrazing indeed varied between annual and perennial species. On the other, this
 242 also indicated that species-specific responses to grazing are mainly determined by
 243 perennial plants (Dorrough *et al.*, 2004).

244 Since species numbers for perennial species are nearly twice of those for annual
 245 species among common species between undisturbed and overgrazed meadow at 3000
 246 and 3200m elevations, it is possible that consistent results for all species and perennial
 247 species, but not for annual species may be attributed to much more species numbers
 248 for perennial species from the perspective of statistic analysis. Thus species-specific
 249 responses to grazing may be not determined by perennial plants. However, at 3400m
 250 and 3600m elevations, although species numbers for annual species are more than
 251 those for perennial species among shared species between undisturbed and overgrazed
 252 madows, we still found consistent results for all species and perennial species, but not
 253 for annual species. Consequently, perennial species but not annual species determine
 254 the response of above- and below-ground traits to overgrazing.

255 As shown in Fig. 4, our data can be used to disentangle different responses to

undisturbed and overgrazed condition between annual and perennial species. Due to N-limitation in undisturbed sites (Zhang *et al.*, 2018), perennial species tend to have high resource conservation strategies. After overgrazing, perennial species are largely removed, whereas annual species largely increased after overgrazing. Thus overgrazing has positive effect on annual species, but negative effect on perennial species. This may force perennial species to change its intrinsic resource conservation into resource acquisition strategy to tolerate overgrazing . In contrast, annual species might be not necessary to make any response for overgrazing.

Conclusion

Together, our results suggested that both above-ground and below-ground traits exhibited similar resource conservation vs. resource acquisition trade-off for responding to overgrazing. Moreover, perennial species but not annual species determine the response of above- and below-ground traits to overgrazing. Our findings also have important implications for the management and recovery of overgrazed meadow ecosystems. First, since,as strong correlations among above-ground traits and below-ground traits can be found in overgrazed meadow, above-ground traits can be a good proxy for below-ground traits, and can be used to understand plant-soil feedbacks and the effects of below-ground traits on ecosystem functioning in overgrazed meadows. Second, since the shift from resource conservation to resource acquisition determine species distribution between undisturbed and overgrazed meadow, selecting species that have high resource acquisition can help the diversification of the overgrazed meadow. Likewise, selecting

desirable species with high resource acquisition to undesirable weeds may help control weeds. Third, since perennial species determine the response of above-ground and below-ground traits to overgrazing, which in turn affect vegetation composition between undisturbed and overgrazed meadow, active seeding of perennial species may lead to strong competition between perennial species and annual species in the overgrazed meadow, which may in turn quickly restore overgrazed meadow to natural condition.

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Reference

- Bergmann J, Ryo M, Prati D, Hempel S, Rillig MC.** 2017. Root traits are more than analogues of leaf traits: the case for diaspore mass. *New Phytologist* **216**, 1130-1139.
- Cingolani AM, Posse G, Collantes MB.** 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology* **42**, 50-59.
- Craine JM, Froehle J, Tilman DG, Wedin DA, Chapin IFS.** 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* **93**, 274-285.
- Díaz S, Noy-Meir I, Cabido M.** 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* **38**, 497-508.

300 **de Bello F, Lepš J, SebastiÀ MT.** 2005. Predictive value of plant traits to grazing
301 along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* **42**,
302 824-833.

303 **de la Riva EG, Marañón T, Pérez-Ramos IM, Navarro-Fernández CM, Olmo M,**
304 **Villar R.** 2018. Root traits across environmental gradients in Mediterranean woody
305 communities: are they aligned along the root economics spectrum? *Plant and Soil* **424**,
306 35-48.

307 **Díaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C,**
308 **Rusch G, Sternberg M, Noy-meir I.** 2007. Plant trait responses to grazing - a global
309 synthesis. *Global Change Biology* **13**, 313-341.

310 **Dong QM, Zhao XQ, Wu GL, Chang XF.** 2015. Optimization yak
311 grazing stocking rate in an alpine grassland of Qinghai-Tibetan Plateau, China.
312 *Environmental Earth Sciences* **73**, 2497-2503.

313 **Dorrough J, Ash J, McIntyre S.** 2004. Plant responses to livestock grazing
314 frequency in an Australian temperate grassland. *Ecography* **27**, 798-810.

315 **Eissenstat D.** 2000. Root structure and function in an ecological context. *New*
316 *Phytologist* **148**, 353-354.

317 **Evju M, Austrheim G, Halvorsen R, Mysterud A.** 2009. Grazing responses in
318 herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem.
319 *Oecologia* **161**, 77-81.

320 **Fort F, Jouany C, Cruz P.** 2013. Root and leaf functional trait relations in
321 Poaceae species: implications of differing resource-acquisition strategies. *Journal of*

322 Plant Ecology **41**, 107-127.

323 **Golodets C, Sternberg M, Kigel J.** 2010. A community-level test of the

324 leaf-height-seed ecology strategy scheme in relation to grazing conditions. Journal of

325 Vegetation Science **20**, 392-402.

326 **Hodge A.** 2004. The plastic plant: root responses to heterogeneous supplies of

327 nutrients. New Phytologist **162**, 9-24.

328 **James M B, Joe F, Mark JS, Jonathan S, Sarah JC, Steve JG, Richard T.** 2001.

329 A plant trait analysis of responses to grazing in a long-term experiment. Journal of

330 Applied Ecology **38**, 253-267.

331 **Laliberté E, Tylianakis JM.** 2012. Cascading effects of long-term land-use changes

332 on plant traits and ecosystem functioning. Ecology **93**, 145-155.

333 **Laliberté E.** 2017. Below-ground frontiers in trait-based plant ecology. New

334 Phytologist **213**, 1597-1603.

335 **Li W, Xu F, Zheng S, Taube F, Bai Y.** 2017. Patterns and thresholds of

336 grazing-induced changes in community structure and ecosystem functioning:

337 species-level responses and the critical role of species traits. Journal of Applied

338 Ecology **54**, 963-975.

339 **Liu G, Freschet GT, Pan X, Cornelissen JHC, Li Y, Dong M.** 2010. Coordinated

340 variation in leaf and root traits across multiple spatial scales in Chinese semi-arid and

341 arid ecosystems. New Phytologist **188**, 543-553.

342 **Mommer L, Weemstra M.** 2012. The role of roots in the resource economics

343 spectrum. New Phytologist **195**, 725-727.

344 **Osnas JLD, Lichstein JW, Reich PB, Pacala SW.** 2013. Global Leaf Trait
345 Relationships: Mass, Area, and the Leaf Economics Spectrum. *Science* **340**, 741-744.

346 **Prieto I, Roumet C, Cardinael R, Dupraz C, Jourdan C, Kim JH, Maeght JL,**
347 **Mao Z, Pierret A, Portillo N.** 2015. Root functional parameters along a land-use
348 gradient: evidence of a community-level economics spectrum. *Journal of Ecology* **103**,
349 361-373.

350 **Reich PB.** 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits
351 manifesto. *Journal of Ecology* **102**, 275-301.

352 **Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N,**
353 **Vrignon-Brenas S, Cao KF, Stokes A.** 2016. Root structure–function relationships in
354 74 species: evidence of a root economics spectrum related to carbon economy. *New*
355 *Phytologist* **210**, 815-826.

356 **Spasojevic MJ, Aicher RJ, Koch GR, Marquardt ES, Mirotchnick N,**
357 **Troxler TG, Collins SL.** 2010. Fire and grazing in a mesic tallgrass prairie:
358 impacts on plant species and functional traits. *Ecology* **91**, 1651-1659.

359 **Stein C, Harpole WS, Suding KN.** 2016. Transitions and invasion along a
360 grazing gradient in experimental California grasslands. *Ecology* **97**, 2319-2330.

361 **Sterck FJ.** 2016. Towards a multidimensional root trait framework: a tree root
362 review. *New Phytologist* **211**, 1159-1169.

363 **Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D.** 2005 Linking leaf
364 and root trait syndromes among 39 grassland and savannah species. *New Phytologist*
365 **167**, 493-508.

366 **Valverde-Barrantes OJ, Blackwood CB.** 2016. Root traits are multidimensional:
367 specific root length is independent from root tissue density and the plant economic
368 spectrum: Commentary on Kramer-Walter et al. *Journal of Ecology* **104**, 1311-1313.

369 **Valverde-Barrantes OJ, Freschet GT, Roumet C, Blackwood CB.** 2017. A
370 worldview of root traits: the influence of ancestry, growth form, climate and
371 mycorrhizal association on the functional trait variation of fine-root tissues in seed
372 plants. *New Phytologist* **215**, 1562-1573.

373 **Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH,**
374 **Wall DH.** 2004. Ecological Linkages Between Aboveground and Belowground
375 Biota. *Science* **304**, 1629-1633.

376 **Weemstra M, Mommer L, Visser EJW, Ruijven J, Kuyper TW, Mohren GMJ,**
377 **Withington JM, Reich PB, Oleksyn J, Eissenstat DM.** 2006. Comparisons of
378 structure and life span in roots and leaves among temperate trees. *Ecological*
379 *Monographs* **76**, 381-397.

380 **Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F,**
381 **Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M.** 2004. The worldwide
382 leaf economics spectrum. *Nature* **428**, 821-827.

383 **Zhang H, Gilbert B, Wang W, Liu J, Zhou S.** 2013. Grazer exclusion alters plant
384 spatial organization at multiple scales, increasing diversity. *Ecology and Evolution* **3**,
385 3604-3612.

386 **Zhang H, John R, Zhu S, Liu H, Xu Q, Qi W, Liu K, Chen HYH, Ye Q.** 2018.
387 Shifts in functional trait–species abundance relationships over secondary subalpine

388 meadow succession in the Qinghai–Tibetan Plateau. *Oecologia* **188**, 547-557.

Figure Legends

Fig. 1. The differences in above-ground traits (height (H; m), leaf maximum photosynthesis rate (A; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and specific leaf area (SLA; cm^2/g) and below-ground traits (root average diameter (RD; mm), root biomass (RB; g), specific root length (SRL; cm/g), specific root area (SRA; cm^2/g) and root tissue density (RTD; g/m^{-3})) between undisturbed and overgrazed meadows for all species and separately for annual and perennial species from 3000 to 3600m elevations. *** and NS (non-significant) indicates $P < 0.001$ and $P > 0.05$, based on Wilcoxon signed-rank tests.

Fig. 2. The interrelationships among above-ground traits (maximum height (H), leaf maximum photosynthesis rate (A) and specific leaf area (SLA)) and below-ground traits (root average diameter (RD), root biomass (RB), specific root length (SRL), specific root area (SRA) and root tissue density (RTD)) in undisturbed and overgrazed meadows for all species, and separately for annuals and perennial species from 3000 to 3600m elevations.

Fig. 3. Principal component analysis for below-ground traits (root average diameter (RD), root biomass (RB), specific root length (SRL), specific root area (SRA) and root tissue density (RTD)) and above-ground traits (height (H), leaf maximum photosynthesis rate (A) and specific leaf area (SLA)) in undisturbed and overgrazed meadows for all species and perennial species from 3000 to 3600m elevations.

Fig. 4. Hypothesized patterns of different responses of annual and perennial species to overgrazing.

Fig. 1.

Fig. 2

Fig. 3

Fig. 4

Annual species

Getting largely increase

No response

No shift from resource acquisition
to resource conservation strategy at both
above-ground and below-ground level

Perennial species

Getting largely removal

Tolerance of overgrazing

A shift from resource acquisition
to resource conservation strategy at both
above-ground and below-ground level