1 **Livestock grazing-induced large-scale biotic homogenization in arid Mediterranean steppe rangelands**

2 Saifi Merdas[1,2]*(ID), Yacine Kouba[3](ID), Tewfik Mostephaoui[1,2](ID), Yassine Farhi[1](ID), Haroun Chenchouni[3,4](ID)

3 [1] Centre of Scientific and Technical Research on Arid Regions, 07000 Biskra, Algeria.

4 [2] Research Centre for Territory Planning, 25000 Constantine, Algeria.

5 [3] Laboratory of Natural Resources and Management of Sensitive Environments 'RNAMS', University of

6 Oum-El-Bouaghi, 04000 Oum-El-Bouaghi, Algeria.

7 [4] Department of Natural and Life Sciences, Faculty of Exact Sciences and Natural and Life Sciences,

8 University of Tebessa, 12002 Tebessa, Algeria.

9

10 * Corresponding author: Saifi Merdas, phone: +213–671-494-261, email: saifieco@gmail.com

11

12 Running title: **Effects of livestock grazing on plant composition and diversity**

13

14 **Competing interests:** The authors declare that they have no competing interests.

15

16 **Availability of data:** The datasets used and/or analyzed during the current study are available from the

17 corresponding author upon reasonable request.

18

23

24 **Authors' contributions: Saifi Merdas**: Conceptualization; Investigation; Resources; Funding acquisition;

25 Formal analysis; Writing - Original Draft; Writing - Review & Editing. **Yacine Kouba**: Conceptualization;

26 Data curation; Formal analysis; Writing - Review & Editing. **Tewfik Mostephaoui**: Investigation;

27 Validation; Writing - Review & Editing. **Yassine Farhi**: Writing - review & editing; Validation. **Haroun**

28 **Chenchouni**: Formal analysis; Visualization; Writing - Original Draft; Writing - Review & Editing.

29  **Abstract**

30  Despite many studies explored the effect of livestock grazing on plant communities the response of species

31  composition and diversity to livestock grazing in arid rangelands remain ambiguous. This study examined the

32  effects of livestock grazing vs grazing exclusion on plant communities in arid steppe rangelands of North

33  Africa. Plant diversity of annual species perennial species and all species combined was measured and

34  compared between grazed and grazing-excluded areas. We also verified whether the difference in plant

35  community composition between the two management types was due to species spatial turnover or community

36  nestedness. Besides the effects of livestock grazing on beta diversity at local among transects and landscape

37  among sites scales were examined using the multiplicative diversity partitioning. Results revealed that livestock

38  grazing significantly decreased the alpha diversity of all species combined and the diversity of annual plants.

39  Livestock grazing induced a shift in plant community composition where the most of species composition

40  variation ~74% was due to infrequent species replacement between the two management types rather than

41  community sub setting ~26%. The analysis of beta diversity at different spatial scales revealed that livestock

42  grazing significantly increased beta diversity at the local scale but decreased it at the landscape scale. Our

43  findings suggest that livestock grazing in arid steppe rangelands increases the variation of plant composition at

44  local spatial scale and engenders vegetation homogeneity at coarse spatial scale. Therefore, the implementation

45  of appropriate management practices such as short-term grazing exclusion is mandatory to prevent these

46  ecosystems from large scale biotic homogenization.

47

48  **Keywords**: Mediterranean rangelands; ecological spatial-scaling; species composition dissimilarity; alpha and

49  beta-diversity; species turnover; rangeland grazing; plant community.

50

51  **1. Introduction**

52      Mediterranean rangelands have evolved for a long time under the effect of grazing and high climatic

53  variability (Perevolotsky & Seligman, 1998; Le Floc'h, 2001). These conditions contributed to the

54  patterning of particular plant communities resilient to perturbations (Perevolotsky & Seligman, 1998;

55  Sternberg et al. 2000). Nonetheless, the excessive use of rangeland resources by grazing and climate

56  change can lead to land degradation (Li et al., 2013). Substantially, the relationship between plant diversity

57   and livestock grazing has been widely studied, especially in arid rangelands (Alrababah et al., 2007; Saiz &

58   Alados, 2014; Wang et al., 2018; Lv et al., 2019). In water-limited ecosystems, grazing is considered the

59   main driver of biodiversity loss and land degradation (Reynolds et al., 2007; Chillo & Ojeda, 2014;

60   Rasmussen et al., 2018). Dry Mediterranean ecosystems are highly heterogeneous (Alados et al., 2006) and

61   complex (Alrababah et al., 2007; Cortina et al., 2009), which requires appropriate and well-adapted

62   measures for sustaining their conservation. This becomes particularly relevant to understand the effect of

63   livestock grazing on plant species composition and diversity in arid rangelands.

64       Despite the considerable number of studies that explored this topic, the response of plant communities to

65   livestock grazing remains controversial. In arid and semi-arid rangelands, environmental filters play a

66   determinant role in the patterning of plant community composition (Fernandez-Gimenez & Allen-Diaz, 1999;

67   Ahlborn et al., 2020). This paradigm is well sustained in the concept of the non-equilibrium model (Illius &

68   O'Connor, 1999; Sullivan & Rohde, 2002). In contrast, low-productivity lands with a long evolutionary

69   history of grazing are characterized by a decline in species diversity following grazing intensity which

70   supports the generalized dynamic equilibrium model (Milchunas et al., 1988; Cingolani et al., 2005). The

71   main ecological concern in the debate between the two models is the definition of the best model that fits the

72   needs of rangeland management. Consequently, the recent development of the debate indicated that both

73   patterns (non-equilibrium – equilibrium) could coexist in the same system (Vetter, 2005; Briske et al., 2020).

74   Nevertheless, the prediction of the response of rangeland dynamics to grazing remains a challenging question

75   (Anderson & Hoffman, 2007; Oñatibia & Aguiar, 2019; Pfeiffer et al., 2019; Gao & Carmel, 2020a). Given

76   the difficulties of management practices in arid environments due to the uncertainties i.e., complex network

77   of interactions between herbivores, environmental factors, and biodiversity, more studies would be necessary

78   to understand thoroughly the interplay between grazers and plant diversity.

79       In the prospect of sustainable resource management, the understanding of the effect of livestock grazing at

80   different spatial scales on plant diversity is needed. Consistently, it has also been reported that grazing changes

81   the distribution of soil nutrients and water, resulting in changes in spatial patterns of the distribution of

82   vegetation (Adler et al., 2001). Therefore, the effects of herbivores on plant diversity, particularly beta-diversity,

83   need to be considered at different spatial scales (Olff & Ritchie, 1998). The application of the multiscale

84   approach is suitable to identify at which scale management practices should be applied (Gabriel et al., 2006;

85    Koyama et al., 2018). Spatial scales with high heterogeneity (beta-diversity) are crucial for the implementation

86    of plant diversity conservation. For example, in dryland ecosystems, Hanke et al. (2014) indicated that

87    functional groups (annuals, perennials) were effective indicators for environmental conservation, and on the

88    landscape scale the vegetation was more heterogeneous. In semi-arid Mediterranean grasslands, however, both

89    local and landscape scales are important for the management of grassland biodiversity (Golodets et al., 2011).

90        North African rangelands extend along the northern edges of the Sahara Desert, which makes these

91    ecosystems subjected to severe effects of the hot-dry desertic climate. These climatic conditions promoted the

92    existence of a specialized plant community (Quézel & Santa, 1963; Slimani et al., 2010; Fatmi et al., 2020).

93    Previous studies on plant communities carried out in these rangelands have mainly focused on the

94    measurement of diversity using species richness, Shannon diversity, and evenness to explain the relationship

95    between livestock grazing and plant diversity (e.g., Amghar et al., 2012; Gamoun et al., 2015; Salemkour et

96    al., 2016; Merdas et al., 2017). However, little information is available on the multi-spatial effects of

97    livestock grazing on community composition, and beta-diversity in these water-limited ecosystems (but see

98    Kouba et al. 2021).

99        Therefore, the main aim of this study is to investigate how livestock grazing affects plant species

100   composition and diversity (alpha- and beta-diversity) in the arid Mediterranean steppe rangelands at fine- and

101   coarse-spatial scales. The detailed objectives of the study are (i) understanding how livestock grazing affects

102   rare, common, and dominant species (*i.e*., alpha diversities) of annual and perennial plants (ii) assessing the

103   effects of livestock grazing on the composition of plant assemblages, and (iii) detecting the effect of livestock

104   grazing on beta-diversity at different spatial scales.

105

106   **2. Materials and methods**

107   *2.1. Study area*

108       The study was conducted, approximately 150 km southeast of the Capital Algiers, in the arid steppes

109   located in Central Algerian rangelands (Fig. 1). The elevation ranges between 621 m a.s.l. in the high plateau

110   region and 980 m in piedmont near the Saharan Atlas, with a mean value of 842 m (± 94.33). Soils of the study

111   area are dominated by Calcimagnesic, carbonated, and encrusted gypsum soils (Halitim, 1988).

112     The climate data obtained from the nearest meteorological station of Bou-Saâda (M'sila Province), for the

113     period of 1988–2014 showed that the climate is arid Mediterranean. The mean annual rainfall was 184 mm with

114     peaks in spring and fall. Only 103 mm of rainfall was recorded during the monitoring year (2014). The average

115     temperature was 32.30°C for July, indicating the hottest month, while January is the coldest month with 8.88°C.

116     The studied plant community is characteristic of the steppe vegetation of North Africa, where Halfah grass

117     *Macrochloa tenacissima* (L.) Kunth (syn. *Stipa tenacissima* L.) dominated. Other common species were shrubs

118     (*Artemisia herba-alba* Asso, *Artemisia campestris* L., *Helianthemum lippii* (L.) Dum. Cours., and *Noaea*

119     *mucronata* (Forssk.) Asch. & Schweinf.), forbs (*Anacyclus monanthos* subsp. *cyrtolepidioides* (Pomel)

120     Humphries, *Atractylis serratuloides* Sieber ex Cass., *Helianthemum salicifolium* (L.) Mill., and *Malva aegyptia*

121     L.) and grasses (*Stipa capensis* Thunb., *Koeleria pubescens* P. Beauv., *Stipa lagascae* Roem. & Schult., and

122     *Poa bulbosa* L.) (Le Houérou, 1995).

123     Lands of the study area are used mainly for livestock grazing where rangelands are subjected to free

124     continuous grazing (all around the year), principally by sheep. The pastoralists are semi-nomadic populations

125     (Slimani et al., 2010). The estimated stocking rate in the study area was 3.77 sheep units/ha, based on the data

126     provided by the agricultural services of M'sila Province; this represents a high-grazing intensity (Merdas et al.,

127     2017). All sampled sites within this region had similar topographic and climate conditions (Kouba et al., 2021).

128     Short-term grazing-exclusion is a management strategy implemented by the High Commission for the

129     Development of the Steppe (HCDS) to maintain the rangelands in a healthy state and avoiding land degradation.

130     The grazing-exclusion areas are open for grazing after pastoral carrying capacity assessment carried out by

131     HCDS technicians. The short-term grazing-exclusion is defined as a period of 3 - 4 years of protection from

132     grazing activity (Sullivan & Rohde, 2002; Amghar et al., 2012; Gamoun, 2014; Gamoun et al., 2015).

133

### 2.2. Data collection

135     In spring 2014, during the period of peak vegetation growth (April-May), the vascular plant species were

136     sampled in ten sites dominated by the Halfah grass (*M. tenacissima*) in the rangelands of Central Algeria. Five

137     sampled sites were freely grazed for decades, whereas five other sites were protected from livestock grazing

138     "grazing-excluded" for the last three years. Within each site, three 200-m linear transects were carried out, which

139     means 15 transects in grazed areas and 15 transects in grazing-excluded areas. Overall, 30 transects were sampled.

140    Plant relative abundance and richness within each transect were estimated using the Point Intercept sampling

141    method (Goodall, 1952), which consists of recording, at every 20 cm intervals, the identity of all individuals that

142    are in contact with a vertical nail (Kouba et al., 2014). The relative abundance of each species in each transect was

143    estimated from the number of individuals recorded along the same transect. Plant species that could not be

144    identified with certainty in the field were collected, pressed, and brought to the laboratory for identification. The

145    plant nomenclature was based on the African Plant Database (www.ville-ge.ch/musinfo/bd/cjb/africa) and the E-

146    flora Maghreb website (https://efloramaghreb.org/).

147

148    *2.3. Plant diversity estimation*

149    Measures of plant diversity, namely, alpha- and beta-diversity were quantified using Hill numbers

150    ($^qD$). Hill's $q$-metrics reflecting the sensitivity of the diversity index to relative abundances of species. The

151    analysis included the following $q$ values: (i) $q=0$ reflects species richness, which is not sensitive to species

152    abundances (ii) $q=1$ is equivalent to the exponential of Shannon entropy index; here, species are weighted

153    in proportion to their frequency in the sampled community, and therefore, it can be interpreted as the

154    number of "typical species" in the community, and (iii) $q=2$ is the equivalent of the inverse of Simpson's

155    concentration index, which can be interpreted as the number of "very abundant species" in the community

156    (Chao et al., 2012; Gossner et al., 2013; Chao et al., 2014).

157

158    *2.4. Statistical analysis*

159    Statistical analysis carried out using the R software (R Core Team, 2020). First, variations in alpha

160    diversity metrics between grazed and grazing-excluded sites were analyzed using generalized linear mixed-

161    effects models (GLMM), for all plant species combined and for annual and perennial species, separately. The

162    GLMMs were performed using the function "lme" of the package {nlme}. To account for spatial dependencies,

163    site location "pseudo-replication" was included as a random effect in the models (Kouba et al., 2015), whereas

164    steppe grazing status "grazed vs. grazing-excluded" was the fixed effect. Normality and homogeneity of

165    variance were tested by examining the model residuals versus the fitted plots and the normal q-q plots of each

166    model.

167    To test for a significant difference in plant species composition between grazed and grazing-excluded areas,

168    PERMANOVA analysis and non-metrical multidimensional scaling (NMDS) ordination were performed using

169    the functions "adonis" and "metaMDS" of the {vegan} package, respectively. NMDS was run based on Bray-

170    Curtis similarities using 4th-root transformation to reduce the weight of the most abundant species. Furthermore,

171    to assess whether the difference in plant species composition was due to species replacement or nestedness, the

172    additive partitioning of the total beta-diversity method (Baselga, 2010) was performed using "beta.sample"

173    function of the package {betapart} (Baselga & Orme, 2012). In this analysis, the total beta-diversity ($\beta_{SOR}$) is

174    defined as a Sørensen dissimilarity index which is additionally partitioned into β Simpson ($\beta_{SIM}$) describing species

175    turnover and β nestedness ($\beta_{SNE}$) which measures community subsetting [$\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$].

176    The effect of grazing on beta-diversity at multiple spatial scales was assessed using multiplicative diversity

177    partitioning (Whittaker, 1972; Jost, 2006, 2007, 2010). This method was mainly employed to quantify among-

178    transects and among-sites beta-diversities for grazed and grazing-excluded steppes. This analysis was

179    performed using the "multipart" function from the {vegan} package.

180

181    **3. Results**

182    *3.1. Species composition and relative abundance*

183    A total of 101 plant species were recorded (Appendix 1) and classified into 81 genera and 26 families. Most

184    species were annuals, *i.e.*, 62 species against 39 perennial species. The grazing-excluded steppes included more

185    species ($S$=93 species) compared to grazed sites ($S$=61 species). Plant species occurring exclusively in grazing-

186    excluded steppes were dominated by annual species (28 out of 40 species). Also, annual species represented 31

187    out of 53 for common species (shared species) whereas they represent 3 out of the 8 species exclusive of grazed

188    steppes (Fig. 2). The most frequent species were *M. tenacissima* (33.25%), *Anacyclus monanthos*

189    *cyrtolepidioides* (11.50%), *Stipa capensis* (7.89%), *Malva aegyptia* (7.67%), and *Artemisia herba-alba*

190    (5.58%).

191

192    *3.2. Alpha diversities*

193    When all species were included in the analysis, all measures of alpha diversity using Hill numbers ($^{q}D$)

194    ($q$=0, $q$=1, $q$=2) were significantly higher in grazing-excluded sites than in grazed areas. The same results were

195   observed for the annual species, except values of the inverse of Simpson concentration ($q$=2) which were not

196   significantly different between steppes. For the perennial species, estimates of plant diversity were not

197   significantly different between grazed and grazing-excluded steppes (Fig. 3).

198

199   *3.3. Beta diversities*

200       The PERMANOVA analysis revealed that plant species composition differed significantly between grazed

201   and grazing-excluded sites ($P$ <0.001). Livestock management type (free grazing vs. grazing-exclusion)

202   explained almost 60% of the variation in the composition of plant communities in arid rangelands. The

203   compositional difference was clear in the plot determined using the NMDS analysis that revealed a clear

204   separation between the grazed and grazing-excluded sites (Fig. 4).

205       Results indicated also that beta-diversity generated from grazed and grazing-excluded sites contributed

206   greatly (54.2%) to the total diversity. Furthermore, the additive partitioning of the overall beta-diversity ($\beta_{SOR}$)

207   indicated that 74.11% of the compositional dissimilarity was due to species turnover whereas 25.89% resulted

208   from nestedness (Table 1). This result reflects that a large part of the compositional differentiation is due to

209   species replacement instead of plant community sub-setting.

210       The multiplicative diversity partitioning also indicated that beta-diversity measures expressed by values of

211   $q$-metrics were higher than expected by chance (Table 2). Among transects, beta-diversity (Beta transects) was

212   higher in grazed areas than in grazing-excluded areas. Whereas, among sites, beta-diversity (Beta sites) was

213   lower in grazed sites compared to grazing-excluded areas. Furthermore, beta-diversity decreased with the

214   increasing of $q$ values in both management types.

215

216   **4. Discussion**

217       Finding from this study highlight the strong connection of plant community diversity to herbivore activity.

218   Plant species diversity of arid steppe rangelands of Algeria decreased significantly in grazed sites where it

219   declined by 30%. Shifts in plant species diversity due to grazing have been previously reported in steppe

220   rangelands of North Africa (Aidoud et al., 2006; Hirche et al., 2011; Salemkour et al., 2016; Kouba et al., 2021).

221   Recently Gao & Carmel (2020b) conducted a meta-analysis on the relationship between grazing and plant

222   diversity and the results showed that in arid environments, diversity responded negatively to grazing intensity.

223　Additionally, in arid Patagonian steppes, intensive grazing stocking rate decreased drastically plant diversity

224　(Oñatibia & Aguiar, 2019). These findings strengthen the assumptions of the generalized dynamic equilibrium

225　model (Milchunas et al., 1988) where grazing intensity decreases plant diversity in more dry conditions.

226　　　Although we found more perennial species in grazing-excluded areas, livestock grazing had not significant

227　effects on rare, frequent, and abundant perennial species. This is mainly due to the fact that the recorded

228　perennial species were among the highly specialized and well-adapted species to specific conditions prevailing

229　in these environments, *i.e*., recurrent drought events and continuous livestock grazing. Particularly, *M.*

230　*tenacissima*, which is considered a grazing-resistant species, was notably abundant in grazed areas in Algerian

231　steppe rangelands (Slimani et al., 2010) and Cabo de Gata Nijar, Spain (Saiz & Alados, 2012).

232　　　This study showed that the richness of annual species in grazing-excluded areas is more important than

233　in grazed steppes. This result is consistent with previous studies carried out in arid Mediterranean rangelands,

234　which reported a high abundance of ephemeral herbaceous species inside the protected areas (Amghar et al.,

235　2012; Louhaichi et al., 2012). Similarly, Neffar et al. (2018) stressed that the rehabilitation of arid steppe

236　rangelands produces more herbage under protection with a high frequency of therophytic annual plants.

237　Overall, it is well acknowledged that the species composition of the Mediterranean rangelands is mainly

238　determined by annual plants with a few numbers of high abundant perennial species such as *M.  tenacissima*

239　(Aidoud et al., 2006; Osem et al., 2007; Salemkour et al., 2016).

240　　　Many annual plants found in the protected areas (e.g., *Scorzonera undulata* Vahl, *Medicago laciniata* (L.)

241　Mill., *Lolium rigidum* Gaudin, *Medicago minima* (L.) L., *Hippocrepis multisiliquosa* L.) are considered as

242　forage species (Le Houérou, 1995), while non-protected areas exposed to free grazing were dominated by

243　undesirable plant species (Oñatibia et al., 2020). This could be attributed to the fact that sheep consume the

244　most nutritious species, which reduces their abundance and even led to their disappearance (Milton & Hoffman,

245　1994; Tarhounin et al., 2010; Oñatibia & Aguiar, 2019). In line with this, Olff & Ritchie (1998) stressed that

246　under the effect of herbivores, grazing-intolerant species can disappear from the community resulting in low

247　diversity.

248　　　Our findings revealed that livestock grazing act as a non-random filter changing significantly the

249　composition of plant assemblages, where the compositional divergence was mainly due to species

250　replacement rather than community sub-setting. On the other hand, our analysis indicated that species

251    turnover affected essentially less frequent species, which means that rare species are the mostly affected ones

252    by livestock overgrazing. Similarly, Li et al. (2015) reported a decrease in the overall plant species richness

253    because the majority of rare species were highly grazed by animals.

254          The analysis of diversity patterns at multiple spatial scales showed that beta-diversity contributed

255    significantly to the overall diversity measure. All measures of beta-diversity (*i.e.*, $q=0$, $q=1$, $q=2$) were

256    significantly different and greater than expected by chance at both coarse and fine spatial scales. This indicates

257    that plant species were not randomly distributed among and within scales, reflecting intraspecific aggregation

258    (Crist et al., 2003). Our analysis also showed that the most important portion of beta-diversity is occurring at a

259    broad scale (*i.e.*, among sites) in both management types (free grazing vs. grazing exclusion). This may be

260    explained as all the combinations of transects beta-diversity could be well represented at the site level could

261    leading to a higher beta-diversity (Beatty, 2014). Moreover, the fact that the values of beta-diversity were the

262    highest when more weight is given to rare species reflects the great emphasis of rare species in patterning plant

263    assemblages in arid steppe rangelands. In the semi-arid Mediterranean rangelands, plant diversity was found to

264    be considerably represented by rare species (Osem et al., 2002). However, the protection from grazing increased

265    the beta-component of the exponential Shannon diversity and the reciprocal Simpson diversity at broad scales

266    (among sites). This can be attributed to the prevention of negative competitive interactions and the establishment

267    of associations between plant species (Dorrough et al. 2007). The results also agree with previous studies that

268    stressed the importance of grazing-exclusion management practice for the conservation of biodiversity in dry areas

269    (Gao & Carmel, (2020b; Kouba et al. 2021). Such pattern of recovery in plant diversity is consistent with theory

270    of the high resilience of Mediterranean rangelands with a long history of grazing (Perevolotsky & Seligman,

271    1998; Golodets et al., 2011).

272          This study demonstrated that livestock grazing in arid rangelands of Algeria increased the compositional

273    divergence in plant communities at fine-scales. This result supports the notion that increased intensity of grazing

274    may surge the spatial variation in species assemblages at the local scale (Zhang et al., 2013). Besides, Golodets

275    et al. (2011) stressed that herbivores increase small scale heterogeneity of soil nutrients (impact of excreta),

276    which may increase plant diversity. Interestingly, our results revealed that livestock grazing reduces

277    compositional divergence and contributes to vegetation homogenization at the landscape scale (*i.e.*, at coarse

278    spatial scale). This finding is in line with other studies that reported a generalization of vegetation

279 homogenization as a result of overgrazing (Dorrough et al., 2007; Li et al., 2015), in particular in arid

280 Mediterranean ecosystems (Jauffret, 2001; Alados et al., 2003, 2004). This biotic homogenization can result in

281 the loss of biodiversity and ecosystem functions (Mori et al. 2018).

282

283 **5. Conclusion**

284 This study highlights the effects of livestock grazing on plant community composition and diversity in arid

285 steppe rangelands, where the land degradation process is complex due to the synergetic interactions between

286 severe climatic conditions and human activities. Our findings suggest that increasing livestock grazing intensity

287 in arid rangelands could decrease plant alpha diversity and induces a shift in plant community composition

288 because of the spatial turnover of less frequent species. Our analysis indicates also that livestock-induced

289 changes in beta-diversity are scale-dependent: at a local scale, these changes are characterized by the increasing

290 variation in species composition, while at the landscape scale they are represented by a large-scale biotic

291 homogenization. We recommend that the improvement of the grazing management system in arid steppe

292 rangelands is mandatory to prevent further land degradation due to biodiversity loss and large-scale biotic

293 homogenization. The implementation of "short-term grazing exclusion" in many sites at the same time and the

294 application of appropriate sheep stocking rates in the surrounding areas could enhance the ecological value of

295 protected steppes.

296

297 **References**

298 Adler, P., Raff, D., Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. Oecologia,

299     128(4), 465–479. https://doi.org/10.1007/s004420100737

300 Ahlborn, J., von Wehrden, H., Lang, B., Römermann, C., Oyunbileg, M., Oyuntsetseg, B., & Wesche, K. (2020).

301     Climate – grazing interactions in Mongolian rangelands: Effects of grazing change along a large-scale

302     environmental gradient. Journal of Arid Environments, 173(May 2019), 104043.

303     https://doi.org/10.1016/j.jaridenv.2019.104043

304 Aidoud, A., Le Floc'h, E., Le Houérou, H.N. (2006). Les steppes arides du nord de l'Afrique. Sécheresse, 17(1-2), 19–30.

305 Alados, C. L., ElAich, A., Papanastasis, V. P., Ozbek, H., & Freitas, H. (2006). Monitoring Tools To Assess Vegetation

306     Successional Regression and Predict Catastrophic Shifts and Desertification in Mediterranean Rangeland

307      Ecosystems. Desertification in the Mediterranean Region. A Security Issue, 429–449. https://doi.org/10.1007/1-

308      4020-3760-0_20

309      Alados, C. L., ElAich, A., Papanastasis, V. P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D.,

310      Cabezudo, B. (2004). Change in plant spatial patterns and diversity along the successional gradient of

311      Mediterranean grazing ecosystems. Ecological Modelling, 180(4), 523–535.

312      https://doi.org/10.1016/j.ecolmodel.2003.10.034

313      Alados, C. L., Pueyo, Y., Giner, M. L., Navarro, T., Escos, J., Barroso, F., Cabezudo, B., Emlen, J. M. (2003).

314      Quantitative characterization of the regressive ecological succession by fractal analysis of plant spatial patterns.

315      Ecological Modelling, 163(1–2), 1–17. https://doi.org/10.1016/S0304-3800(02)00294-6

316      Alrababah, M. A., Alhamad, M. A., Suwaileh, A., Al-Gharaibeh, M. (2007). Biodiversity of semi-arid Mediterranean

317      grasslands: Impact of grazing and afforestation. Applied Vegetation Science, 10(2), 257–264.

318      https://doi.org/10.1111/j.1654-109X.2007.tb00524.x

319      Amghar, F., Forey, E., Margerie, P., Langlois, E., Brouri, L., Kadi-Hanifi, H. (2012). Grazing exclosure and plantation:

320      A synchronic study of two restoration techniques improving plant community and soil properties in arid degraded

321      steppes (Algeria). Revue Ecologie Terre et Vie, 67(3), 257–269.

322      Anderson, P. M. L., & Hoffman, M. T. (2007). The impacts of sustained heavy grazing on plant diversity and

323      composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South

324      Africa. Journal of Arid Environments, 70(4), 686–700. https://doi.org/10.1016/j.jaridenv.2006.05.017

325      Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and

326      Biogeography, 19(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

327      Baselga, A., Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. Methods in Ecology and

328      Evolution, 3(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

329      Beatty, S. W. (2014). Habitat Heterogeneity and Maintenance of Species in Understory Communities. In: Gilliam, F.S.,

330      Roberts, M.R. (Ed.), The Herbaceous Layer in Forests of Eastern North America. (pp. 215–232). Oxford University

331      Press. https://doi.org/10.1093/acprof:osobl/9780199837656.003.0008

332      Briske, D. D., Coppock, D. L., Illius, A. W., & Fuhlendorf, S. D. (2020). Strategies for global rangeland stewardship:

333      Assessment through the lens of the equilibrium–non-equilibrium debate. Journal of Applied Ecology, 57(6), 1056–

334      1067. https://doi.org/10.1111/1365-2664.13610

335  Chao, A., Chiu, C. H., Hsieh, T. C., Inouye, B. D. (2012). Proposing a resolution to debates on diversity partitioning.

336      Ecology, 93(9), 2037–2051. https://doi.org/10.1890/11-1817.1

337  Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., Ellison, A. M. (2014). Rarefaction and

338      extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecological

339      Monographs, 84(1), 45–67. https://doi.org/10.1890/13-0133.1

340  Chillo, V., Ojeda, R. (2014). Disentangling ecosystem responses to livestock grazing in drylands. Agriculture,

341      Ecosystems and Environment, 197, 271–277. https://doi.org/10.1016/j.agee.2014.08.011

342  Cingolani, A. M., Noy-meir, I., & Díaz, S. (2005). Grazing Effects on Rangeland Diversity: a Synthesis of

343      Contemporary Models. Ecological Applications, 15(2), 757–773. https://doi.org/10.1890/03-5272

344  Cortina, J., Maestre, F. T., & Ramírez, D. (2009). Innovations in semiarid restoration. The case of Stipa tenacissima L.

345      steppes. Land Restoration to Combat Desertification: Innovative Approaches, Quality Control and Project

346      Evaluation, 121–144.

347  Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S. (2003). Partitioning Species Diversity across

348      Landscapes and Regions: A Hierarchical Analysis of α, β, and γ Diversity. American Naturalist, 162(6),

349      734–743. https://doi.org/10.1086/378901

350  Dorrough, J. W., Ash, J. E., Bruce, S., McIntyre, S. (2007). From plant neighbourhood to landscape scales: How

351      grazing modifies native and exotic plant species richness in grassland. Plant Ecology, 191(2), 185–198.

352      https://doi.org/10.1007/s11258-006-9236-y

353  Fatmi, H., Mâalem, S., Harsa, B., Dekak, A., Chenchouni, H. (2020). Pollen morphological variability correlates with a

354      large-scale gradient of aridity. Web Ecology, 20, 19–32. https://doi.org/10.5194/we-20-19-2020

355  Fernandez-Gimenez, M. E., & Allen-Diaz, B. (1999). Testing a non-equilibrium model of rangeland vegetation

356      dynamics in Mongolia. Journal of Applied Ecology, 36(6), 871–885. https://doi.org/10.1046/j.1365-

357      2664.1999.00447.x

358  Gabriel, D., Roschewitz, I., Tscharntke, T., Thies, C. (2006). Beta diversity at different spatial scales: Plant communities

359      in organic and conventional agriculture. Ecological Applications, 16(5), 2011–2021. https://doi.org/10.1890/1051-

360      0761(2006)016[2011:bdadss]2.0.co;2

361  Gamoun, M. (2014). Grazing intensity effects on the vegetation in desert rangelands of Southern Tunisia. Journal of

362      Arid Land, 6(3), 324–333. https://doi.org/10.1007/s40333-013-0202-y

363  Gamoun, M., Patton, B., Hanchi, B. (2015). Assessment of vegetation response to grazing management in arid

364      rangelands of southern Tunisia. International Journal of Biodiversity Science, Ecosystem Services and

365      Management, 11(2), 106–113. https://doi.org/10.1080/21513732.2014.998284

366  Gao, J., & Carmel, Y. (2020a). A global meta-analysis of grazing effects on plant richness. Agriculture, Ecosystems and

367      Environment, 302(August 2019), 107072. https://doi.org/10.1016/j.agee.2020.107072

368  Gao, J., & Carmel, Y. (2020b). Can the intermediate disturbance hypothesis explain grazing–diversity relations at a

369      global scale? Oikos, 129(4), 493–502. https://doi.org/10.1111/oik.06338

370  Golodets, C., Kigel, J., Sternberg, M. (2011). Plant diversity partitioning in grazed Mediterranean grassland at multiple

371      spatial and temporal scales. Journal of Applied Ecology, 48(5), 1260–1268. https://doi.org/10.1111/j.1365-

372      2664.2011.02031.x

373  Goodall, D. W. (1952). Some considerations in the use of point quadrats for the analysis of vegetation. Australian

374      Journal of Scientific Research Ser B: Biological Sciences, 5, 1–41. https://doi.org/10.1071/BI9520001

375  Gossner, M. M., Getzin, S., Lange, M., Pašalić, E., Türke, M., Wiegand, K., Weisser, W. W. (2013). The importance of

376      heterogeneity revisited from a multiscale and multitaxa approach. Biological Conservation, 166, 212–220.

377      https://doi.org/10.1016/j.biocon.2013.06.033

378  Halitim, A. (1988). Sols des régions arides d'Algérie. Edition OPU, Algiers, Algeria.

379  Hanke, W., Böhner, J., Dreber, N., Jürgens, N., Schmiedel, U., Wesuls, D., Dengler, J. (2014). The impact of livestock

380      grazing on plant diversity: an analysis across dryland ecosystems and scales in southern Africa. Ecological

381      Applications, 24(5), 1188–1203. https://doi.org/10.1890/13-0377.1

382  Hirche, A., Salamani, M., Abdellaoui, A., Benhouhou, S., Valderrama, J. M. (2011). Landscape changes of

383      desertification in arid areas: the case of south-west Algeria. Environmental Monitoring and Assessment, 179(1–4),

384      403–420. https://doi.org/10.1007/s10661-010-1744-5

385  Illius, A. W., & O'Connor, T. G. (1999). On the Relevance of Nonequilibrium Concepts to Arid and Semiarid Grazing

386      Systems. Ecological Applications, 9(3), 798. https://doi.org/10.2307/2641330

387  Jauffret, S. (2001). Validation et comparaison de divers indicateurs des changements à long term dans les écosystèmes

388      méditerranéens arides : application au suivi de la désertification dans le Sud tunisien. Doctoral thesis, University of

389      Aix-Marseille.

390  Jost, L. (2006). Entropy and Diversity. Oikos, 113(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

391   Jost, L. (2007). Partitioning Diversity into Independent Alpha and Beta Components. Ecology, 88(10), 2427–2439.

392       https://doi.org/10.1073/pnas.0807060105

393   Jost, L. (2010). Independence of alpha and beta diversities. Ecology, 91(7), 1969–1974. https://doi.org/10.1890/09-

394       0368.1

395   Kouba, Y., Martínez-García, F., de Frutos, Á., Alados, C. L. (2014). Plant β-diversity in human-altered forest

396       ecosystems: the importance of the structural, spatial, and topographical characteristics of stands in patterning plant

397       species assemblages. European Journal of Forest Research, 133(6), 1057–1072. https://doi.org/10.1007/s10342-

398       014-0822-6

399   Kouba, Y., Martínez-García, F., De Frutos, Á., Alados, C. L. (2015). Effects of previous land-use on plant species

400       composition      and      diversity      in      Mediterranean      forests.      PLoS      ONE,      10(9).

401       https://doi.org/10.1371/journal.pone.0139031

402   Kouba, Y., Merdes, S., Mostephaoui, T., Saadali, B., Chenchouni, H. (2021). Plant community composition and

403       structure under short-term grazing exclusion in steppic arid rangelands. Ecological Indicators, 120, 106,910. https://

404       doi.org/10.1016/j.ecolind.2020.106910

405   Koyama, A., Koyanagi, T. F., Akasaka, M., Kusumoto, Y., Hiradate, S., Takada, M., Okabe, K. (2018). Partitioning the

406       plant   diversity   of   semi-natural   grasslands   across   Japan.   Oryx,   52(3),   471–478.

407       https://doi.org/10.1017/S0030605316001526

408   Le Floc'h, E. (2001). Biodiversité et gestion pastorale en zones arides et semi-arides méditerranéennes du Nord de l '

409       Afrique. Bocconea, 13, 223–237.

410   Le Houérou, H. N. (1995). Bioclimatologie et biogéographie des steppes arides du Nord de l'Afrique : diversité

411       biologique, développement durable et désertisation. In : Le Houérou H.-N. (ed.). Bioclimatologie et biogéographie

412       des steppes arides du Nord de l'Afrique : diversité biologique. Options Méditerranéennes : Série B. Etudes et

413       Recherches, 10, 396. http://om.ciheam.org/om/pdf/b10/CI951183.pdf

414   Li, W., Zhan, S., Lan, Z., Ben Wu, X., Bai, Y. (2015). Scale-dependent patterns and mechanisms of grazing-induced

415       biodiversity loss: evidence from a field manipulation experiment in semiarid steppe. Landscape Ecology, 30(9),

416       1751–1765. https://doi.org/10.1007/s10980-014-0146-4

417   Li, X. L., Gao, J., Brierley, G., Qiao, Y. M., Zhang, J., & Yang, Y. W. (2013). Rangeland Degradation On The Qinghai-

418       Tibet   Plateau:   Implications   For   Rehabilitation.   Land   Degradation   and   Development,   24(1),   72–80.

419       https://doi.org/10.1002/ldr.1108

420  Louhaichi, M., Ghassali, F., Salkini, A. K., & Petersen, S. L. (2012). Effect of sheep grazing on rangeland plant

421       communities: Case study of landscape depressions within Syrian arid steppes. *Journal of Arid Environments*, *79*,

422       101–106. https://doi.org/10.1016/j.jaridenv.2011.11.024

423  Lv, S., Yan, B., Wang, Z., Han, G., Kang, S. (2019). Grazing intensity enhances spatial aggregation of dominant species

424       in a desert steppe. Ecology and Evolution, 9(10), 6138–6147. https://doi.org/10.1002/ece3.5197

425  Merdas, S., Menad, A., Mostephaoui, T., Sakaa, B. (2017). Plant community structure and diversity under grazing

426       gradient in arid Mediterranean steppe of Algeria. Journal of Materials and Environmental Science, 8(12), 4329–

427       4338. https://doi.org/10.26872/jmes.2017.8.12.456

428  Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A Generalized Model of the Effects of Grazing by Large

429       Herbivores on Grassland Community Structure. The American Naturalist, 132(1), 87–106.

430       https://doi.org/10.1086/284839

431  Milton, S. J., Hoffman, M. T. (1994). The application of state-and-transition models to rangeland research and

432       management in Arid Succulent and Semi-Arid Grassy Karoo, South Africa. African Journal of Range and Forage

433       Science, 11(1), 18–26. https://doi.org/10.1080/10220119.1994.9638349

434  Mori, A. S., Isbell, F., Seidl, R. (2018). β-Diversity, Community Assembly, and Ecosystem Functioning. Trends in

435       Ecology and Evolution, 33(7), 549–564. https://doi.org/10.1016/j.tree.2018.04.012

436  Neffar, S., Menasria, T., Chenchouni, H. (2018). Diversity and functional traits of spontaneous plant species in Algerian

437       rangelands rehabilitated with prickly pear (*Opuntia ficus-indica* L.) plantations. Turkish Journal of Botany, 42(4),

438       448–461. https://doi.org/10.3906/bot-1801-39

439  Olff, H., Ritchie, M. E. (1998). Effects of herbivores on Grassland Plant Diversity. Trends in Ecology and Evolution,

440       13(7), 261–265. https://doi.org/10.1016/S0169-5347(98)01364-0

441  Oñatibia, G. R., Amengual, G., Boyero, L., & Aguiar, M. R. (2020). Aridity exacerbates grazing-induced rangeland

442       degradation: A population approach for dominant grasses. Journal of Applied Ecology, 57(10), 1999–2009. https://

443       doi.org/10.1111/1365-2664.13704

444  Oñatibia, G. R., Aguiar, M. R. (2019). Grasses and grazers in arid rangelands: Impact of sheep management on forage

445       and non-forage grass populations. Journal of Environmental Management, 235, 42–50.

446       https://doi.org/10.1016/j.jenvman.2019.01.037

447  Osem, Y., Perevolotsky, A., & Kigel, J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid

448  rangeland: Interactions with small-scale spatial and temporal variation in primary productivity. Journal of

449  Ecology, 90(6),                936–946.                https://doi.org/10.1046/j.1365-2745.2002.00730.x.

451  Osem, Y., Perevolotsky, A., & Kigel, J. (2007). Interactive effects of grazing and shrubs on the annual plant community

452  in semi-arid Mediterranean shrublands. Journal of Vegetation Science, 18(6), 869. https://doi.org/10.1658/1100-

453  9233(2007)18[869:ieogas]2.0.co;2

454  Perevolotsky, A., & Seligman, N. G. (1998). Role of grazing in Mediterranean rangeland ecosystems. BioScience,

455  48(12), 1007–1117. https://doi.org/10.2307/1313457

456  Pfeiffer, M., Langan, L., Linstädter, A., Martens, C., Gaillard, C., Ruppert, J. C., Higgins, S. I., Mudongo, E. I., &

457  Scheiter, S. (2019). Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – Insights from a

458  trait-based      dynamic      vegetation      model.      Ecological      Modelling,      395,      11–22.

459  https://doi.org/10.1016/j.ecolmodel.2018.12.013

460  Quézel, P., Santa, S. (1963). Nouvelle flore d'Algérie et des régions désertiques méridionales. Tome 2, CNRS, Paris.

461  R Core Team (2020). R: A language and environment for statistical computing. R foundation for statistical computing.

462  http://www.R-project.org

463  Rasmussen, K., Brandt, M., Tong, X., Hiernaux, P., Diouf, A. A., Assouma, M. H., Tucker, C. J., Fensholt, R. (2018).

464  Does grazing cause land degradation? Evidence from the sandy Ferlo in Northern Senegal. Land Degradation and

465  Development, 29(12), 4337–4347. https://doi.org/10.1002/ldr.3170

466  Reynolds, J. F., Smith, D. M. S., Lambin, E. F., Turner B. L., I. I., Mortimore, M., Batterbury, S. P. J., Downing, T. E.,

467  et al. (2007). Global Desertification: Building a Science for Dryland Development. Science, 316, 847–851.

468  http://doi.org/10.1126/science.1131634

469  Saiz, H., Alados, C. L. (2012). Changes in semi-arid plant species associations along a livestock grazing gradient. PLoS

470  ONE, 7(7), 1–9. https://doi.org/10.1371/journal.pone.0040551

471  Saiz, H., Alados, C. L. (2014). Effect of livestock grazing in the partitions of a semiarid plant-plant spatial signed

472  network. Acta Oecologica, 59, 18–25. https://doi.org/10.1016/j.actao.2014.05.006

473  Salemkour, N., Aidoud, A., Chalabi, K., Chefrour, A. (2016). Évaluation des effets du contrôle de pâturage dans des

474  parcours steppiques arides en Algérie. Revue Ecologie Terre et Vie, 71(2), 178–191.

475     Slimani, H., Aidoud, A., Rozé, F. (2010). 30 Years of protection and monitoring of a steppic rangeland undergoing

476         desertification. Journal of Arid Environments, 74(6), 685–691. https://doi.org/10.1016/j.jaridenv.2009.10.015

477     Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E. D., & Kigel, J. (2000). Vegetation response to grazing

478         management in a Mediterranean herbaceous community: A functional group approach. Journal of Applied

479         Ecology, 37(2), 224–237. https://doi.org/10.1046/j.1365-2664.2000.00491.x

480     Sullivan, S., & Rohde, R. (2002). On non-equilibrium in arid and semi-arid grazing systems. Journal of Biogeography,

481         29(12), 1595–1618. https://doi.org/10.1046/j.1365-2699.2002.00799.x

482     Tarhounin, M., Salem, F. Ben, Belgacem, A. O., Neffati, M. (2010). Acceptability of plant species along grazing

483         gradients around watering points in Tunisian arid zone. Flora, 205(7), 454–461.

484         https://doi.org/10.1016/j.flora.2009.12.020

485     Vetter, S. (2005). Rangelands at equilibrium and non-equilibrium: Recent developments in the debate. Journal of Arid

486         Environments, 62(2), 321–341. https://doi.org/10.1016/j.jaridenv.2004.11.015

487     Wang, X., Song, N., Yang, X., Wang, L., Chen, L. (2018). Grazing exclusion-induced shifts, the relative importance of

488         environmental filtering, biotic interactions and dispersal limitation in shaping desert steppe communities, northern

489         China. Journal of Arid Land, 10(3), 402–415. https://doi.org/10.1007/s40333-018-0411-5

490     Whittaker, R. H. (1972). Evolution and Measurement of Species Diversity. Taxon, 21(2/3), 213–251.

491     Zhang, H., Gilbert, B., Wang, W., Liu, J., Zhou, S. (2013). Grazer exclusion alters plant spatial organization at multiple

492         scales, increasing diversity. Ecology and Evolution, 3(10), 3604–3612. https://doi.org/10.1002/ece3.743

493

494   **Table 1.** Additive partitioning of the overall beta-diversity generated from grazed and grazing-excluded areas

495   ($\beta_{SOR}$) to spatial turnover ($\beta_{SIM}$) and nestedness ($\beta_{SNE}$) components ($\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$). $\beta_{SIM}$: the value of the turnover

496   component, measured as Simpson dissimilarity; $\beta_{SNE}$: the value of the nestedness component, measured as the

497   nestedness-resultant fraction of Sørensen dissimilarity; $\beta_{SOR}$: the value of the overall beta-diversity, measured as

498   Sorensen dissimilarity.

|                          | $\beta_{SIM}$ | $\beta_{SNE}$ | $\beta_{SOR}$ |
|--------------------------|---------------|---------------|---------------|
| Values                   | 0.40          | 0.14          | 0.54          |
| Percentage of the total  | 74.12         | 25.88         | 100           |

499

500

501

502

503

504

505

506

507

508

509

510

511

512

513

514

515

516

517

518

519 **Table 2.** Comparing beta-diversities (*i.e.*, among-transects "Beta transects" and among-sites "Beta sites")

520 between grazed and grazing-excluded areas in the steppe rangelands of Algeria. Diversity was quantified using

521 the Hill numbers ($^qD$), with $q=0$ (all species are given equal weight), $q=1$ (greater weight is given to common

522 species), or $q=2$ (greater weight is given to dominant species). Deviations from null distributions (numbers

523 within brackets) are expressed by dividing the observed values by the expected values.

| $q$-metrics (Hill numbers) | Free grazed steppes | | Grazing-excluded steppes | |
|---|---|---|---|---|
| | Beta transects | Beta sites | Beta transects | Beta sites |
| $q = 0$ | 1.68 (1.22) | 1.88 (1.43) | 1.66 (1.20) | 1.98 (1.45) |
| $q = 1$ | 1.23 (1.18) | 1.40 (1.37) | 1.15 (1.10) | 1.49 (1.46) |
| $q = 2$ | 1.18 (1.18) | 1.10 (1.10) | 1.04 (1.04) | 1.31 (1.31) |

524
525
526
527
528
529