

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

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

**Conflict of interest:** The authors declare that there is no conflict of interest.

**Availability of data:** The datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

**Acknowledgments and Funding:** The authors acknowledge the support of the Algerian Directorate General for Scientific Research and Technological Development (DGRSDT) via the Centre for Scientific and Technical Research on Arid Regions (CRSTRA). The authors also thank the High Commission for the Development of the Steppe (HCDS) for the technical support during field surveys.

**CRedit Authors' contributions:** **Saifi Merdas:** Conceptualization; Investigation; Resources; Funding acquisition; Formal analysis; Writing - Original Draft; Writing - Review & Editing. **Yacine Kouba:** Conceptualization; Data curation; Formal analysis; Writing - Review & Editing. **Tewfik Mostephaoui:** Investigation; Validation; Writing - Review & Editing. **Yassine Farhi:** Validation; Writing - review & editing. **Haroun Chenchouni:** Visualization; Validation; Writing - Original Draft; Writing - Review & Editing.

## Abstract

Despite many studies explored the effect of livestock grazing on plant communities, the response of species composition and diversity to livestock grazing in arid rangelands remain ambiguous. This study examined the effects of livestock grazing on plant communities in arid steppe rangelands of North Africa. Plant diversity of annual species, perennial species and all species combined was measured and compared between grazed and grazing-excluded areas. We also examined the relative importance of species turnover and community nestedness. Moreover, the effects of livestock grazing on beta diversity at local among transects and landscape among sites scales were examined using the multiplicative diversity partitioning. Results revealed that livestock grazing significantly decreased the alpha diversity of all species combined and the diversity of annual plants. Livestock grazing induced a shift in plant community composition where most of species composition variation (~74%) was due to infrequent species replacement 'turnover' between the two management types rather than nestedness (~26%). Results revealed also that among transects, beta diversity was higher in grazed steppes than in grazing-excluded steppes. Whereas, among sites, beta diversity was lower in grazed steppes compared to grazing-excluded steppes. These findings suggest that livestock grazing in arid steppe rangelands increases the variation in plant species composition at a local spatial scale and engenders vegetation homogeneity at landscape spatial scale. Therefore, the implementation of appropriate management practices such as short-term grazing exclusion is mandatory to prevent these ecosystems from large scale biotic homogenization.

**KEYWORDS:** Mediterranean rangelands; ecological spatial-scaling; species composition dissimilarity; alpha and beta diversity; species turnover; rangeland grazing; plant community.

## 1 | INTRODUCTION

Unsustainable livestock farming is considered the biggest driver of biodiversity loss and land productivity decline in drylands (Hanke et al., 2014). The impact of grazing on plant community structure and diversity, particularly in arid rangelands, is a major concern for range use and nature conservation (Fischer et al., 2019). Many studies carried out in these ecosystems have focused on the effects of grazing on alpha diversity which is an important focus because biodiversity is likely more affected at that scale. However other components of biodiversity, mainly beta diversity which is defined as the difference in species composition between communities, can also be altered due to grazing disturbances (Grman et al., 2018). For instance, de Bello et al, (2007) stressed that species beta diversity could respond to grazing intensity in different ways (positively, unimodal-response, or negatively) depending on climatic conditions (from arid to humid conditions).

Recent studies have revealed that livestock grazing behaviour could affect vegetation patterns in a distinct way across spatial scales (Limb et al., 2018). At a local scale, grazing disturbance might increase species diversity, by decreasing competitiveness and favouring the colonization of new species (Dorrough et al., 2007). On a broad scale, however, grazing could decrease diversity by eliminating species that are not adapted to grazing (Fischer et al., 2019; Limb et al., 2018). Furthermore, intense grazing could promote the expansion of certain plant species in a particular location. These species may have different functional roles, auto-ecological characteristics and adaptation strategies, including colonizer and invader species, ephemerals, ruderals, and even stabilizer species (such as the dominant species in semi-arid steppe rangelands of North Africa: *Macrochloa tenacissima* (L.) Kunth (syn. *Stipa tenacissima* L.), *Artemisia herba-alba* Asso, *Artemisia campestris* L., *Atriplex halimus* L. and *Stipagrostis pungens* (Desf.) De Winter. This leads to the selection of more similar species, which engenders compositional convergence, a process known as biological homogenization (Puhl et al., 2014). This process promotes the substitution of native species by widespread generalists that have greater ecological plasticity and wider ecological niche (Puhl et al., 2014). In arid and semi-arid rangelands, ruderals and therophytic plants govern the biotic homogenization in plant communities. Because the ecological plasticity of these plant categories allow species to cope with rapid environmental changes (Tarhouni et al., 2010; Kouba et al., 2021). Despite this broad conceptual context, a full understanding of how grazing affects the biodiversity of arid rangelands still lacking. The reason behind this is that most of the existing studies did not consider concomitantly different diversity measures and different spatial scales (Hanke et al., 2014).

Other studies have revealed that species diversity alone may not adequately reflect the shifts in vegetation composition and structure that occur in response to grazing disturbance in the dryland biomes, changes of the vegetation might be better reflected by trait-based diversity measures (Hanke et al., 2014, Puhl et al., 2014). This includes the exploration of aspects beyond taxonomic diversity patterns such as the measurement of  $\alpha$ ,  $\beta$ , and  $\gamma$  components of plant functional and phylogenetic diversity (Crist et al., 2003; Wang et al., 2019). As the timing of species establishment and possibly competitive outcomes are determined by functional traits linked to life-history strategies such as life longevity (Byun et al., 2013; Puhl et al., 2014). To understand community dynamics, it is critical to monitor shifts in the diversity of functional groups based on relevant traits (Puhl et al., 2014).

North African rangelands extend along the northern edges of the Sahara Desert, which makes these ecosystems subjected to severe effects of the hot-dry desertic climate. These climatic conditions promoted the existence of a specialized plant community (Slimani et al., 2010; Fatmi et al., 2020). Previous studies on plant communities carried out in these rangelands have mainly focused on the measurement of diversity using species richness, Shannon diversity, and evenness to explain the relationship between livestock grazing and plant diversity (e.g., Amghar et al., 2012; Merdas et al., 2017). However, little information is available on how livestock grazing affects species composition and beta diversity at multiple spatial scales in these arid ecosystems (Kouba et al., 2021).

In the present study, ten alfa steppes were selected in the arid high plains of Algeria, to investigate the response of plant community structure and diversity to grazing disturbance. We contrast freely grazed and grazing-excluded steppes to address the following questions: (i) does livestock grazing evenly affects rare, common, and dominant species (i.e., alpha diversities) of annual and perennial plants? (2) does the grazing-induced change in species composition due to species turnover (species restitution i.e. species eliminated by grazing and replaced) or community nestedness (refers to habitats with low richness host part of the species of richer habitats) or both of

them? (3) how livestock grazing affects plant beta diversity at different spatial scales (local scale vs. landscape scale)? Based on the assumption that plant diversity responds negatively to grazing under resource-poor conditions (Milchunas & Lauenroth, 1993), we expect negatives responses of alpha and beta diversities to livestock grazing in these arid steppes. Furthermore, based on previous studies carried out in the arid high plains of Algeria (Aidoud et al., 2006, Amghar et al., 2012, Kouba et al., 2021) we predict that livestock grazing will alter the composition of plant assemblages mainly by inducing the loss and replacement of many native species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was conducted, approximately 150 km southeast of the capital Algiers, in the arid steppes located in Central Algerian rangelands (Figure 1). The elevation ranges between 621 m a.s.l. in the high plateau region and 980 m in piedmont near the Saharan Atlas, with a mean value of 842 m ( $\pm 94.33$ ). Soils of the study area are dominated by Calcimagnesic, carbonated, and encrusted gypsum soils (Halitim, 1988).

The climate data obtained from the nearest meteorological station of Bou-Saâda (M'sila Province), for the period of 1988–2014 showed that the climate is arid Mediterranean. The mean annual rainfall was 184 mm with peaks in spring and fall. Only 103 mm of rainfall was recorded during the monitoring year (2014). The average temperature was 32.30°C for July, indicating the hottest month, while January is the coldest month with 8.88°C.

The studied plant community is characteristic of the steppe vegetation of North Africa, where Halfah grass *Macrochloa tenacissima* (syn. *Stipa tenacissima*) dominated. Other common species were shrubs (*Artemisia herba-alba* Asso, *Artemisia campestris* L., *Helianthemum lippii* (L.) Dum. Cours., and *Noaea mucronata* (Forssk.) Asch. & Schweinf.), forbs (*Anacyclus monanthos* subsp. *cyrtolepidioides* (Pomel) Humphries, *Atractylis serratuloides* Sieber ex Cass., *Helianthemum salicifolium* (L.) Mill., and *Malva aegyptia* L.) and grasses (*Stipa capensis* Thunb., *Koeleria pubescens* P. Beauv., *Stipa lagascae* Roem. & Schult., and *Poa bulbosa* L.) (Le Houérou, 1995).

Lands of the study area are used mainly for livestock grazing where rangelands are subjected to free continuous grazing (all around the year), principally by sheep. The pastoralists are semi-nomadic populations (Slimani et al., 2010). The estimated stocking rate in the study area was 3.77 sheep units/ha, based on the data provided by the agricultural services of M'sila Province; this represents a high-grazing intensity (Merdas et al., 2017). All sampled sites within this region had similar topographic and climate conditions (Kouba et al., 2021). Short-term grazing-exclusion is a management strategy implemented by the High Commission for the Development of the Steppe (HCDS) to maintain the rangelands in a healthy state and avoiding land degradation. The grazing-exclusion areas are open for grazing after pastoral carrying capacity assessment carried out by HCDS technicians. The short-term grazing-exclusion is defined as a period of 3–4 years of protection from grazing activity (Sullivan & Rohde, 2002; Amghar et al., 2012).

### 2.2 | Data collection

In spring 2014, during the period of peak vegetation growth (April–May), the vascular plant species were sampled in ten sites dominated by the Halfah grass (*M. tenacissima*) in the rangelands of Central Algeria (see Kouba et al., 2021 for details on characteristics of the sampled sites). Five sampled sites were freely grazed for decades, whereas five other sites were protected from livestock grazing “grazing-excluded” for the last three years (from 2011). Within each site, we performed vegetation surveys in three 200 m-long transects spaced 250 m apart, which means 15 transects in grazed areas and 15 transects in grazing-excluded areas. Plant species abundance, richness and composition were estimated for each transect using the line-point intercept method, which consists of recording, at every 20 cm intervals (i.e., 1000 points located every 20 cm), the identity of all individuals that are in contact with a vertical nail (Kouba et al., 2014). The abundance of each species in each transect was estimated from the number of individuals recorded along the same transect. Plant species that could not be identified with certainty in the field were collected, pressed, and brought to the herbarium for identification.

The plant nomenclature was based on the African Plant Database ([www.ville-ge.ch/musinfo/bd/cjb/africa](http://www.ville-ge.ch/musinfo/bd/cjb/africa)) and the E-flora Maghreb website (<https://efloramaghreb.org/>).

## 2.3 | Plant diversity estimation

Measures of plant diversity, namely, alpha- and beta-diversity were quantified using Hill numbers ( $^qD$ ). Hill's  $q$ -metrics reflecting the sensitivity of the diversity index to relative abundances of species. The analysis included the following  $q$  values: (i)  $q=0$  reflects species richness, which is not sensitive to species abundances (ii)  $q=1$  is equivalent to the exponential of Shannon entropy index; here, species are weighted in proportion to their frequency in the sampled community, and therefore, it can be interpreted as the number of "typical species" in the community, and (iii)  $q=2$  is the equivalent of the inverse of Simpson's concentration index, which can be interpreted as the number of "very abundant species" in the community (Chao et al., 2012).

## 2.4 | Statistical analysis

Statistical analysis was carried out using the R software (R Core Team, 2020). First, variations in alpha diversity metrics between grazed and grazing-excluded sites were analyzed using generalized linear mixed-effects models (GLMM), for all plant species combined and for annual and perennial species, separately. The GLMMs were performed using the function "lme" of the package {nlme}. To account for spatial dependencies, site location "pseudo-replication" was included as a random effect in the models (Kouba et al., 2015), whereas steppe grazing status "grazed vs. grazing-excluded" was the fixed effect. Normality and homogeneity of variance were tested by examining the model residuals versus the fitted plots and the normal  $q$ - $q$  plots of each model.

To test for a significant difference in plant species composition between grazed and grazing-excluded areas, PERMANOVA analysis and non-metrical multidimensional scaling (NMDS) ordination were performed using the functions "adonis" and "metaMDS" of the {vegan} package, respectively. NMDS was run based on Bray-Curtis similarities using 4<sup>th</sup>-root transformation to reduce the weight of the most abundant species. Furthermore, to assess whether the difference in plant species composition was due to species replacement or nestedness, the additive partitioning of the total beta diversity method (Baselga, 2010) was performed using "beta.sample" function of the package {betapart} (Baselga & Orme, 2012). In this analysis, the total beta diversity ( $\beta_{SOR}$ ) is defined as a Sørensen dissimilarity index which is additionally partitioned into  $\beta$  Simpson ( $\beta_{SIM}$ ) describing species turnover and  $\beta$  nestedness ( $\beta_{SNE}$ ) which measures community subsetting [ $\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$ ].

The effect of grazing on beta diversity at multiple spatial scales was assessed using multiplicative diversity partitioning (Jost, 2006). This method was mainly employed to quantify among-transects (Beta transects) and among-sites (Beta transects) beta diversities for grazed and grazing-excluded steppes. At transect level (grain = transect and extent = site),  $\beta$ -diversity measures reflect within sites variations (i.e., local variation in species composition). At site level (grain = site and extent = management type {grazed/grazing-excluded}),  $\beta$ -diversity measures reflect among sites within management type variation. Multiplicative diversity partitioning analysis was performed using the "multipart" function from the {vegan} package.

# 3 | RESULTS

## 3.1 | Species composition and relative abundance

A total of 101 plant species were recorded (Appendix 1) and classified into 81 genera and 26 families. Most species were annuals, i.e., 62 species against 39 perennial species. The grazing-excluded steppes included more species ( $S=93$  species) compared to grazed sites ( $S=61$  species). Plant species occurring exclusively in grazing-excluded steppes were dominated by annual species (28 out of 40 species). Also, annual species represented 31 out of 53 for common species (shared species) whereas they represent 3 out of the 8 species exclusive of grazed steppes (Figure 2). The most frequent species were *M. tenacissima* (33.25%), *Anacyclus monanthos* (11.50%), *Stipa capensis* (7.89%), *Malva aegyptia* (7.67%), and *Artemisia herba-alba* (5.58%).

## 3.2 | Alpha diversities

When all species were included in the analysis, all measures of alpha diversity using Hill numbers ( ${}^qD$ ) ( $q=0$ ,  $q=1$ ,  $q=2$ ) were significantly higher in grazing-excluded sites than in grazed areas. The same results were observed for the annual species, except values of the inverse of Simpson concentration ( $q=2$ ) which were not significantly different between steppes. For the perennial species, estimates of plant diversity were not significantly different between grazed and grazing-excluded steppes (Figure 3).

### 3.3 | Beta diversities

The PERMANOVA analysis revealed that plant species composition differed significantly between grazed and grazing-excluded sites ( $P<0.001$ ). Livestock management type (free grazing vs. grazing-exclusion) explained almost 60% of the variation in the composition of plant communities in arid rangelands. The compositional difference was clear in the plot determined using the NMDS analysis that revealed a clear separation between the grazed and grazing-excluded sites (Figure 4).

Results indicated also that beta diversity generated from grazed and grazing-excluded sites contributed greatly (54.2%) to the total diversity. Furthermore, the additive partitioning of the overall beta diversity ( $\beta_{SOR}$ ) indicated that 74.11% of the compositional dissimilarity was due to species turnover whereas 25.89% resulted from nestedness. This result reflects that a large part of the compositional differentiation is due to species replacement instead of plant community nestedness.

The multiplicative diversity partitioning also indicated that beta diversity measures expressed by values of  $q$ -metrics were higher than expected by chance (Figure 5). Among transects, beta diversity (Beta transects) was higher in grazed areas than in grazing-excluded areas. Whereas, among sites, beta diversity (Beta sites) was lower in grazed sites compared to grazing-excluded areas. Furthermore, beta diversity decreased with the increasing of  $q$  values in both management types.

## 4 | DISCUSSION

### 4.1 | Influence of grazing on over all diversity

Finding from this study highlight the strong connection of plant community diversity to herbivore activity. Plant species diversity of arid steppe rangelands of Algeria decreased significantly in grazed sites where it declined by 30%. Shifts in plant species diversity due to grazing have been previously reported in steppe rangelands of North Africa (Aidoud et al., 2006; Hirche et al., 2011; Kouba et al., 2021). Recently Gao & Carmel (2020a) conducted a meta-analysis on the relationship between grazing and plant diversity and the results showed that in arid environments, diversity responded negatively to grazing intensity. These findings strengthen the assumptions of the generalized dynamic equilibrium model (Milchunas et al., 1988) where grazing intensity decreases plant diversity in dry conditions. Livestock grazing can play a non-negligible role in the loss of biodiversity and the collapse of ecosystem services under a changing climate especially when rangelands are overloaded with livestock animals exceeding the carrying capacity (Hao et al., 2018; Oñatibia et al., 2020). However, long-term grazing under moderate intensity has driven increases in plant species richness of temperate grasslands with no losses of native plants and biodiversity (Puhl et al., 2014).

Although we found more perennial species in grazing-excluded areas, livestock grazing had no significant effects on rare, frequent, and abundant perennial species. This is mainly because the recorded perennial species were among the highly specialized and well-adapted species to the specific ecological conditions prevailing in these environments, *i.e.*, recurrent drought events and continuous livestock grazing. Particularly, *M. tenacissima*, which is considered a grazing-resistant species and barely palatable, was notably abundant in grazed areas in Algerian steppe rangelands (Slimani et al., 2010) and Cabo de Gata Nijar, Spain (Saiz & Alados, 2012). The effects of grazing on plant diversity differ from one climatic region to another (Milchunas & Lauenroth, 1993). While the aridity and severe climatic conditions deepen the degradation of rangelands due to grazing in arid and semi-arid regions (Oñatibia et al., 2020; Kouba et al., 2021); in temperate regions, moderate grazing can promote plant diversity. According to Puhl et al. (2014), grazing in the mesophytic prairies increased local species richness by 46% and regional richness by 28%.

## 4.2 | Alpha diversity

This study showed that the richness of annual species in grazing-excluded areas is higher than in grazed steppes. This result is consistent with previous studies carried out in arid Mediterranean rangelands, which reported a high abundance of ephemeral herbaceous species inside the protected areas (Amghar et al., 2012). Similarly, Neffar et al. (2018) stressed that the rehabilitation of arid steppe rangelands produces more herbage under protection with a high frequency of therophytic annual plants. Overall, it is well acknowledged that the species composition of the Mediterranean rangelands is mainly determined by annual plants with a few numbers of high abundant perennial species such as *M. tenacissima* (Aidoud et al., 2006; Osem et al., 2007).

Many annual plants found in the protected areas (e.g., *Scorzonera undulata* Vahl, *Medicago laciniata* (L.) Mill., *Lolium rigidum* Gaudin, *Medicago minima* (L.) L., *Hippocrepis multisiliquosa* L.) are considered as forage species (Le Houérou, 1995), while non-protected areas exposed to free grazing were dominated by undesirable plant species (Oñatibia et al., 2020). This could be attributed to the fact that sheep preferably consume the most nutritious species, which reduces their abundance and even led to their disappearance (Tarhouni et al., 2010). In line with this, Olff & Ritchie (1998) stressed that under the effect of herbivores, grazing-intolerant species can disappear from the community resulting in low diversity.

Our findings revealed that livestock grazing changed significantly the composition of plant assemblages, where the compositional divergence was mainly due to species replacement (74%) rather than community nestedness (26%). Indeed, a total of 40 species (70% annuals and 30% perennials) present exclusively in grazing-excluded steppes replaced the 8 exclusive species (37.5% annuals and 62.5% perennials) of grazed steppes. On the other hand, our analysis indicated that transient species are the most affected by livestock grazing. Similarly, Li et al. (2015) reported a decrease in the overall plant species richness because the majority of rare species were highly grazed by animals. The data of this study indicated that the rarest species (frequency of occurrence in samples ranged between 3.3–6.7%) that were absent in grazed steppes include 14 annuals (*Adonis dentata*, *Ammoides verticillata*, *Avena sterilis*, *Centaurea omphalotricha*, *Ebenus pinnata*, *Echinaria capitata*, *Filago germanica*, *Hippocrepis multisiliquosa*, *Lolium rigidum*, *Medicago minima*, *Papaver hybridum*, *Reseda luteola*, *Rochelia disperma*, and *Spergularia diandra*) and 9 perennials (*Asparagus albus*, *Atractylis delicatula*, *Centaurea incana*, *Centaurea tenuifolia*, *Erodium glaucophyllum*, *Genista microcephala*, *Peganum harmala*, *Salvia verbenaca*, and *Thymelaea hirsuta*).

## 4.3 | Beta diversity

The analysis of diversity patterns at multiple spatial scales showed that beta diversity contributed significantly to the overall diversity measure. All measures of beta diversity (*i.e.*,  $q=0$ ,  $q=1$ ,  $q=2$ ) were significantly different and greater than random estimates at both landscape and local spatial scales. This indicates that plant species were not randomly distributed among and within scales, reflecting intraspecific aggregation (Crist et al., 2003). Our analysis also showed that the most important portion of beta diversity is occurring at a broad scale (*i.e.*, among sites) in both management types (free grazing vs. grazing exclusion). This may be explained as all the combinations of transects beta diversity could be well represented at the site level could leading to a higher beta diversity (Beatty, 2014). Moreover, the fact that the values of beta diversity were the highest when more weight is given to rare species reflects the great emphasis of rare species in patterning plant assemblages in arid steppe rangelands. In the semi-arid Mediterranean rangelands, plant diversity was found to be considerably represented by rare species (Osem et al., 2002). However, the protection from grazing increased the beta component of the exponential Shannon diversity and the reciprocal Simpson diversity at broad scales (among sites). This can be attributed to the prevention of negative competitive interactions and the establishment of associations between plant species (Dorrough et al., 2007). The results also agree with previous studies that stressed the importance of grazing-exclusion management practice for the conservation of biodiversity in dry areas (Gao & Carmel, 2020b; Kouba et al., 2021). Such pattern of recovery in plant diversity is consistent with the theory of the high resilience of Mediterranean rangelands with a long history of grazing (Perevolotsky & Seligman, 1998; Golodets et al., 2011).

This study demonstrated that livestock grazing in arid rangelands of Algeria increased the compositional divergence in plant communities. This result supports the notion that increased intensity of grazing may surge the spatial variation in species assemblages at the local scale (Zhang et al., 2013). Besides, Golodets et al. (2011) stressed that herbivores increase small scale heterogeneity of soil nutrients (impact of excreta), which may increase plant diversity. Interestingly, our results revealed that livestock grazing reduces compositional divergence and contributes to vegetation homogenization at the landscape scale. This finding is in line with other studies that reported a generalization of vegetation homogenization as a result of overgrazing (Dorrough et al., 2007; Li et al., 2015), in particular in arid Mediterranean ecosystems (Alados et al., 2004). This plant homogenization can result in the loss of biodiversity and ecosystem functions (Mori et al., 2018).

## 5 | CONCLUSION

This study highlights the effects of livestock grazing on plant community composition and diversity in arid steppe rangelands. Our findings suggest that increasing livestock grazing intensity in arid rangelands could decrease plant alpha diversity and induces a shift in plant community composition because of the spatial turnover of less frequent species. Our analysis indicates also that livestock-induced changes in beta diversity are scale-dependent: at a local scale, these changes are characterized by the increasing variation in species composition, while at the landscape scale they are represented by a large-scale biotic homogenization. We recommend that the improvement of the grazing management system in arid steppe rangelands is mandatory to prevent further land degradation due to biodiversity loss and large-scale biotic homogenization. The implementation of “short-term grazing exclusion” in many sites at the same time and the application of appropriate sheep stocking rates in the surrounding areas could enhance the ecological value of protected steppes.

## REFERENCES

- Aidoud, A., Le Floch, E., & Le Houérou, H.N. (2006). Les steppes arides du nord de l'Afrique. *Sécheresse*, 17(1–2), 19–30.
- Alados, C. L., ElAich, A., Papanastasis, V. P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D., & Cabezudo, B. (2004). Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecological Modelling*, 180(4), 523–535. <https://doi.org/10.1016/j.ecolmodel.2003.10.034>
- Amghar, F., Forey, E., Margerie, P., Langlois, E., Brouri, L., & Kadi-Hanifi, H. (2012). Grazing enclosure and plantation: A synchronic study of two restoration techniques improving plant community and soil properties in arid degraded steppes (Algeria). *Revue Ecologie Terre et Vie*, 67(3), 257–269.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Beatty, S. W. (2014). Habitat Heterogeneity and Maintenance of Species in Understory Communities. In: Gilliam, F.S., Roberts, M.R. (Ed.), *The Herbaceous Layer in Forests of Eastern North America*. (pp. 215–232). Oxford University Press. <https://doi.org/10.1093/acprof:osobl/9780199837656.003.0008>
- Byun, C., de Blois, S., & Brisson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, 101(1), 128–139. <https://doi.org/10.1111/1365-2745.12016>
- Chao, A., Chiu, C. H., Hsieh, T. C., & Inouye, B. D. (2012). Proposing a resolution to debates on diversity partitioning. *Ecology*, 93(9), 2037–2051. <https://doi.org/10.1890/11-1817.1>
- Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning Species Diversity across Landscapes and Regions: A Hierarchical Analysis of  $\alpha$ ,  $\beta$ , and  $\gamma$  Diversity. *American Naturalist*, 162(6), 734–743. <https://doi.org/10.1086/378901>
- de Bello, F., Lepš, J., & Sebastià, M.-T. (2007). Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. *Journal of Vegetation Science*, 18(1), 25. [https://doi.org/10.1658/1100-9233\(2007\)18\[25:geotsr\]2.0.co;2](https://doi.org/10.1658/1100-9233(2007)18[25:geotsr]2.0.co;2)

- 335 Fatmi, H., Mâalem, S., Harsa, B., Dekak, A., & Chenchouni, H. (2020). Pollen morphological variability correlates with  
336 a large-scale gradient of aridity. *Web Ecology*, 20, 19–32. <https://doi.org/10.5194/we-20-19-2020>
- 337 Fischer, F. M., Bonnet, O. J. F., Cezimbra, I. M., & Pillar, V. D. (2019). Long-term effects of grazing intensity on  
338 strategies and spatial components of functional diversity in subtropical grassland. *Applied Vegetation Science*,  
339 22(1), 39–47. <https://doi.org/10.1111/avsc.12402>
- 340 Gao, J., & Carmel, Y. (2020a). A global meta-analysis of grazing effects on plant richness. *Agriculture, Ecosystems and*  
341 *Environment*, 302, 107072. <https://doi.org/10.1016/j.agee.2020.107072>
- 342 Gao, J., & Carmel, Y. (2020b). Can the intermediate disturbance hypothesis explain grazing–diversity relations at a global  
343 scale?. *Oikos*, 129(4), 493–502. <https://doi.org/10.1111/oik.06338>
- 344 Golodets, C., Kigel, J., & Sternberg, M. (2011). Plant diversity partitioning in grazed Mediterranean grassland at multiple  
345 spatial and temporal scales. *Journal of Applied Ecology*, 48(5), 1260–1268. <https://doi.org/10.1111/j.1365-2664.2011.02031.x>
- 347 Grman, E., Zirbel, C. R., Bassett, T., & Brudvig, L. A. (2018). Ecosystem multifunctionality increases with beta  
348 diversity in restored prairies. *Oecologia*, 188, 837–848. <https://doi.org/10.1007/s00442-018-4248-6>
- 349 Halitim, A. (1988). *Sols des régions arides d'Algérie*. Edition OPU, Algiers, Algeria.
- 350 Hanke, W., Böhner, J., Dreber, N., Jürgens, N., Schmiedel, U., Wesuls, D., & Dengler, J. (2014). The impact of livestock  
351 grazing on plant diversity: an analysis across dryland ecosystems and scales in southern Africa. *Ecological*  
352 *Applications*, 24(5), 1188–1203. <https://doi.org/10.1890/13-0377.1>
- 353 Hao, L., Pan, C., Fang, D., Zhang, X., Zhou, D., Liu, P., ... & Sun, G. (2018). Quantifying the effects of overgrazing  
354 on mountainous watershed vegetation dynamics under a changing climate. *Science of the Total Environment*,  
355 639, 1408–1420. <https://doi.org/10.1016/j.scitotenv.2018.05.224>
- 356 Hirche, A., Salamani, M., Abdellaoui, A., Benhouhou, S., & Valderrama, J. M. (2011). Landscape changes of  
357 desertification in arid areas: the case of south-west Algeria. *Environmental Monitoring and Assessment*, 179(1–4),  
358 403–420. <https://doi.org/10.1007/s10661-010-1744-5>
- 359 Jost, L. (2006). Entropy and Diversity. *Oikos*, 113(2), 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- 360 Kouba, Y., Martínez-García, F., de Frutos, Á., & Alados, C. L. (2014). Plant  $\beta$ -diversity in human-altered forest  
361 ecosystems: the importance of the structural, spatial, and topographical characteristics of stands in patterning plant  
362 species assemblages. *European Journal of Forest Research*, 133(6), 1057–1072. <https://doi.org/10.1007/s10342-014-0822-6>
- 364 Kouba, Y., Martínez-García, F., De Frutos, Á., & Alados, C. L. (2015). Effects of previous land-use on plant species  
365 composition and diversity in Mediterranean forests. *PLoS ONE*, 10(9).  
366 <https://doi.org/10.1371/journal.pone.0139031>
- 367 Kouba, Y., Merdes, S., Mostephaoui, T., Saadali, B., & Chenchouni, H. (2021). Plant community composition and  
368 structure under short-term grazing exclusion in steppic arid rangelands. *Ecological Indicators*, 120, 106,910.  
369 <https://doi.org/10.1016/j.ecolind.2020.106910>
- 370 Le Houérou, H. N. (1995). Bioclimatologie et biogéographie des steppes arides du Nord de l'Afrique: diversité  
371 biologique, développement durable et désertisation. In : Le Houérou H.-N. (ed.). Bioclimatologie et biogéographie  
372 des steppes arides du Nord de l'Afrique: diversité biologique. Options Méditerranéennes: Série B. Etudes et  
373 Recherches, 10, 396. <http://om.ciheam.org/om/pdf/b10/CI951183.pdf>
- 374 Li, W., Zhan, S., Lan, Z., Ben Wu, X., & Bai, Y. (2015). Scale-dependent patterns and mechanisms of grazing-induced  
375 biodiversity loss: evidence from a field manipulation experiment in semiarid steppe. *Landscape Ecology*, 30(9),  
376 1751–1765. <https://doi.org/10.1007/s10980-014-0146-4>
- 377 Limb, R. F., Hovick, T. J., Norland, J. E., & Volk, J. M. (2018). Grassland plant community spatial patterns driven by herbivory  
378 intensity. *Agriculture, Ecosystems and Environment*, 257, 113–119. <https://doi.org/10.1016/j.agee.2018.01.030>
- 379 Merdas, S., Menad, A., Mostephaoui, T., & Sakaa, B. (2017). Plant community structure and diversity under grazing  
380 gradient in arid Mediterranean steppe of Algeria. *Journal of Materials and Environmental Science*, 8(12), 4329–  
381 4338. <https://doi.org/10.26872/jmes.2017.8.12.456>
- 382 Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A Generalized Model of the Effects of Grazing by  
383 Large Herbivores on Grassland Community Structure. *The American Naturalist*, 132(1), 87–106.  
384 <https://doi.org/10.1086/284839>



- Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 63(4), 327–366. <https://doi.org/10.2307/2937150>
- Mori, A. S., Isbell, F., & Seidl, R. (2018).  $\beta$ -Diversity, Community Assembly, and Ecosystem Functioning. *Trends in Ecology and Evolution*, 33(7), 549–564. <https://doi.org/10.1016/j.tree.2018.04.012>
- Neffar, S., Menasria, T., & Chenchouni, H. (2018). Diversity and functional traits of spontaneous plant species in Algerian rangelands rehabilitated with prickly pear (*Opuntia ficus-indica* L.) plantations. *Turkish Journal of Botany*, 42(4), 448–461. <https://doi.org/10.3906/bot-1801-39>
- Olf, H., & Ritchie, M. E. (1998). Effects of herbivores on Grassland Plant Diversity. *Trends in Ecology and Evolution*, 13(7), 261–265. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)
- Oñatibia, G. R., Amengual, G., Boyero, L., & Aguiar, M. R. (2020). Aridity exacerbates grazing-induced rangeland degradation: A population approach for dominant grasses. *Journal of Applied Ecology*, 57(10), 1999–2009. <https://doi.org/10.1111/1365-2664.13704>
- Osem, Y., Perevolotsky, A., & Kigel, J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: Interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology*, 90(6), 936–946. <https://doi.org/10.1046/j.1365-2745.2002.00730.x>
- Osem, Y., Perevolotsky, A., & Kigel, J. (2007). Interactive effects of grazing and shrubs on the annual plant community in semi-arid Mediterranean shrublands. *Journal of Vegetation Science*, 18(6), 869. [https://doi.org/10.1658/1100-9233\(2007\)18\[869:ieogas\]2.0.co;2](https://doi.org/10.1658/1100-9233(2007)18[869:ieogas]2.0.co;2)
- Perevolotsky, A., & Seligman, N. G. (1998). Role of grazing in Mediterranean rangeland ecosystems. *BioScience*, 48(12), 1007–1117. <https://doi.org/10.2307/1313457>
- Puhl, L. E., Perelman, S. B., Batista, W. B., & Burkart, S. E. (2014). Local and regional long-term diversity changes and biotic homogenization in two temperate grasslands. *Journal of Vegetation Science*, 25(5), 1278–1288. <https://doi.org/10.1111/jvs.12179>
- R Core Team (2020). R: A language and environment for statistical computing. R foundation for statistical computing. <http://www.R-project.org>
- Saiz, H., & Alados, C. L. (2012). Changes in semi-arid plant species associations along a livestock grazing gradient. *PLoS ONE*, 7(7), 1–9. <https://doi.org/10.1371/journal.pone.0040551>
- Slimani, H., Aidoud, A., & Rozé, F. (2010). 30 Years of protection and monitoring of a steppic rangeland undergoing desertification. *Journal of Arid Environments*, 74(6), 685–691. <https://doi.org/10.1016/j.jaridenv.2009.10.015>
- Sullivan, S., & Rohde, R. (2002). On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography*, 29(12), 1595–1618. <https://doi.org/10.1046/j.1365-2699.2002.00799.x>
- Tarhouni, M., Ben Salem, F., Ouled Belgacem, A., & Neffati, M. (2010). Acceptability of plant species along grazing gradients around watering points in Tunisian arid zone. *Flora*, 205(7), 454–461. <https://doi.org/10.1016/j.flora.2009.12.020>
- Wang, J., Chen, C., Li, J., Feng, Y., & Lu, Q. (2019). Different ecological processes determined the alpha and beta components of taxonomic, functional, and phylogenetic diversity for plant communities in dryland regions of Northwest China. *PeerJ*, 6, e6220. <https://doi.org/10.7717/peerj.6220>
- Zhang, H., Gilbert, B., Wang, W., Liu, J., & Zhou, S. (2013). Grazer exclusion alters plant spatial organization at multiple scales, increasing diversity. *Ecology and Evolution*, 3(10), 3604–3612. <https://doi.org/10.1002/ece3.743>

## FIGURE LEGENDS

**FIGURE 1.** Location of the study area in the central steppe rangelands of Algeria. Orange solid points (●) indicate locations of sampled sites in grazed steppes and green solid points (●) represent grazing-excluded sites

**FIGURE 2.** Plant relative abundance (in%) and species richness for perennials and annuals in grazed and grazing-excluded steppe rangelands of arid lands of Algeria.

**FIGURE 3.** Comparing alpha diversities for all plant species combined, perennials and annuals, between grazed and grazing-excluded “ungrazed” areas of the steppe rangelands of Algeria. Results of GLMMs tests are included in the figure as an asterisk (\*) indicating significant differences ( $P > 0.05$ ), and (ns) no significant differences

**FIGURE 4.** Non-metrical multidimensional scaling (NMDS) ordination based on Bray-Curtis similarities using 4th-root transformation. Each symbol-point represents a 200-m transect used in plant sampling.

**FIGURE 5.** Comparing beta diversities between grazed and grazing-excluded in the arid steppes rangelands of Algeria. Diversity was quantified using the Hill numbers, with  $q = 0$  (all species are given equal weight),  $q = 1$  (greater weight is given to common species), or  $q = 2$  (greater weight is given to dominant species). “Beta transects GS” and “Beta transects GES” refer to among transects beta diversity (grain = transect and extent = site) in grazed and grazing-excluded steppes, respectively; “Beta sites GS” and “Beta sites GES” refer to among sites beta diversity (grain = site and extent = management type) in grazed and grazing-excluded steppes, respectively.