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Responses of individual plant species, functional groups, *α*- and *β*-diversity to short-term grazing exclusion under severe drought episode in long-term grazed Alfa-steppes

YACINE KOUBA[1*], SAIFI MERDES[2,3], BADREDDINE SAADALI[4], AND HAROUN CHENCHOUNI[5,6]

[1]Department of Geography and Land Planning, University of Larbi Ben M'hidi, Oum El Bouaghi 04000 Algeria.

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

[3] Laboratory of Biology and Environment, Department of Biology and Ecology, Mentouri Brothers University, Constantine 25017 Algeria.

[4]Department of Geology, University of Larbi Ben M'hidi, Oum El Bouaghi 04000 Algeria.

[5]Department of Natural and Life Sciences, University of Tebessa, Tebessa 12002 Algeria.

[6]Laboratory of Natural Resources and Management of Sensitive Environments 'RNAMS', University of Larbi Ben M'hidi, Oum-El-Bouaghi 04000 Algeria.

*Corresponding author. Email: kouba.yacine@univ-oeb.dz

Abstract. Grazing exclusion has been proved to be one of the main measures for rehabilitating degraded arid steppes. However, the effect of this management practice on plant species diversity and composition is ambiguous, specially under prolonged droughts. Concurrently considering the responses of individual plant species, diversity of functional groups, α-diversity, and β-diversity (and its components) may be crucial to the holistic understanding of grazing exclusion effects on plant communities under drought conditions. Here, we investigated the response of these diversity measures to short-term sheep exclusion under severe drought episode in arid steppes of Alfa-grass (*Stipa tenacissima*) with a long evolutionary history of livestock grazing. Individual species responses were tested based on species occurrence and abundance in either grazed or grazing-excluded steppes, in addition, we used indicator species analysis to assess the strength of the association between plant species and management type. Likewise, α-diversity, abundance- and incidence-based β-diversity, as well as the functional groups' diversities were quantified using Hill Numbers and compared between the two management types. Sheep grazing exclusion enabled the recovery of various Alfa-steppe indicator species and improved the size of regional species pool, overall α-diversity, and the diversity of therophytes. This management practice decreased the abundance-based β-diversity and the nestedness-resultant fraction of the incidence-based β-diversity at the local scale, while at the landscape scale increased the abundance-based β-diversity and its balanced variation fraction and reduced the incidence-based β-diversity and its turnover component. Furthermore, protection from grazing altered β-diversities scaling patterns by maintaining higher balanced variation in species abundance at large spatial scale and greater abundance-gradient in species composition at the fine-scale. Our results suggest that the implementation of short-term grazing exclusion in degraded arid steppes would be the appropriate management practice for vegetation restoration and plant diversity conservation during prolonged drought periods.

Key words: Mediterranean steppes; drylands; alpha diversity; beta diversity; rangeland grazing; indicator species.

INTRODUCTION

Rangelands occupy a vast area of terrestrial ecosystems (ca. 30 %; Ellis and Ramankutty 2008) and are not only a valuable base for livestock production but also provide important ecological services such as water infiltration and storage, erosion control, wildlife habitat biodiversity, and carbon sequestration (Reinhart et al. 2018, Vecchio et al. 2019). Currently, many rangelands are degrading over the world as a result of non-sustainable grazing management and global warming (Cipriotti et al. 2019). Thereby, rangelands degradation has become a serious issue and how to restore degraded rangelands is currently one of the major focuses of ecologists and land managers (Li et al. 2018).

Improving grazing management practices is viewed as a fundamental approach to restore degraded rangelands (Mekuria and Aynekulu 2011, Jones 2013). A variety of management strategies have been implemented to restore degraded rangelands worldwide (Neffar et al. 2018), but the most fundamental and economic management practice remain a nature-based solution “grazing exclusion”, especially in arid and semiarid regions (Tang et al. 2016), due to its low investment, extensiveness, simple implementation, and quick response .

The effect of short- or long-term grazing exclusion on plant communities of arid rangelands has been the focus of several recent studies. Some of them have found that short-term exclusion increases the richness and diversity of plant species (Zhang and Zhao 2015, Ebrahimi et al. 2016, Liu et al. 2019), plant cover and density (Al-Rowaily et al. 2015, Tang et al. 2016, Li et al. 2018), and affects plant composition (Korkanç 2014). While, other studies have suggested that grazing exclusion does not have any significant effect on vegetation coverage (Kakinuma et al. 2017), or have negative effects on species richness and diversity (Yao et al. 2019). Thus, the response of plant communities to grazing exclusion in arid rangelands are inconsistent and hotly debated (Frank et al. 2014). One possible reason for the inconsistent results is a failure to consider the impacts of climatic conditions. For example, drought frequency and intensity may greatly affect vegetation dynamics in arid rangelands and the stochastic nature of precipitation may obfuscate vegetation response patterns to grazing exclusion in these ecosystems (Kakinuma et al. 2017).

Yet, there has been a little consideration of whether the response of plant communities to grazing exclusion is species-specific or functionally identity-dependent, likewise a general understanding of the reaction of β-diversity, at different spatial scales, to the removal of livestock grazing is still missing in arid rangelands, despite an extensive theoretical background. Furthermore, the responses of individual plant species, functional groups' diversities, α-diversity, and β-diversity (and its components) to grazing exclusion have never been tackled simultaneously in one study. Although, the concurrent investigation of the effects of grazing exclusion on these community-related metrics may yield important insights for vegetation restoration and plant diversity conservation in arid rangelands.

Steppe rangelands of North Africa in general and Alfa (*Stipa tenacissima* L.) steppes in particular are considered among the most threatened biomes of the word (Slimani et al. 2010, Carapeto and Véla 2018). These steppes cover c. 32,000 km^2 (Bautista et al. 2009), which are the remains of an estimated 86,500 km^2 area covered by these steppes some decades ago (Le Houérou 1995). Ecologically, Alfa steppes are of great importance due to their biological potential and the crucial role they play in soil protection and fighting against desertification (Le Houérou 1995, Cerdà 1997, Khouane 2018). Essentially there are two driving forces that shape the structure, diversity and composition of plant communities in these ecosystems, on the one hand the frequency and intensity of droughts, and on the other hand livestock grazing pressure (Slimani et al. 2010).

Short-term grazing exclusion has been widely implemented during the last decades to restore degraded steppes in the north African countries (Jeddi and Chaieb 2010, Amghar et al. 2016) . However, there is scarce field evidence from these steppes about the effects of grazing exclusion on plant communities, particularly under severe drought episodes. Therefore, this study examined the effect of short-term sheep grazing exclusion on plant communities' diversity and composition under severe drought episode in Alfa steppes with a long evolutionary history of livestock grazing. The objectives of this study were: (1) to understand the individual species' responses to grazing exclusion and to identify a set of exclosure-indicator species; (2) to clarify whether the responses of plant functional groups (selected based on growth forms, life span, and Raunkiaer life-forms) to short-term grazing exclusion under severe drought are identity-dependent and whether the new environmental conditions alter the interactions between the functional groups; and finally, (3) to test whether the responses of incidence- and abundance-based β-diversity (and their components) to short-term exclusion are expressed at local scale and/or at landscape scale and to clarify whether protection from grazing affects scaling patterns of β-diversity components.

MATERIAL AND METHODS

Study area

The experimental area is located in the arid steppe rangelands of Algeria near the province of Msila (Fig. 1). The mean elevation of the area is 842 (±94.33) and slope averages 3.66° (±1.88°) (Table 1). Soils are dominated by Calcimagnesic, carbonated, and encrusted gypsum soils.

The climate of the area is arid because of the continental effects from the Sahara Desert (Gorczynski continentality index=25.9). According to long-term meteorological data (1988–2014), mean temperatures of the region averaged 20 °C, where mean maximum temperatures reached 32°C in July and August. The mean minimum temperatures (~8°C) were recorded in December and January when occasional periods of subfreezing surface temperature occurred. The annual average rainfall was 184mm, most of it occurred during spring and fall. The dry period extended over almost ten months a year (from mid-January to mid-November). It should be noted that the irregular distribution of rainfall in space and time has historically determined land uses of these rangelands.

The area includes collective grazing rangelands characterizing by steppic (low-height and sparse) vegetation with the dominance of the Alfa grass "*S. tenacissima*" (a stable form of degradation of dry Mediterranean sclerophylic forests) mixed with some shrubs (ex. *Artemisia herba-alba*, *A. campestris*, *Helianthemum lippii* and *Noaea mucronate*), forbs (ex. *Anacyclus cyrtolepidioides*, *Atractylis serratuloides*, *H. salicifolium* and *Malva aegyptiaca*) and grasses (ex. *S. tortilis*, *Koeleria pubescens*, *S. lagascae* and *Poa bulbosa*).

Historically, herders have adopted nomadic practices, which helped maintain healthy steppes by implementing grazing rotation while avoiding overgrazing. Nevertheless, the more recent sedentary land-use leads to overgrazing supported by the massive use of cheap fodder which has increased sharply the number of sheep in these arid steppes (Martínez-Valderrama et al. 2018).

In order to cope with land degradation and biodiversity loss, the Algerian government started in 1994 a strategic program for the restoration of degraded steppe rangelands. Short-term grazing exclusion from sheep grazing was a widely used technique by the High Commission for the Development of the Steppe (HCDS) to assist and boost natural regeneration mainly on lesser degraded steppes (Amghar et al. 2012). This technique consists of the set-up of boundary stones around the selected area for protection and a local salaried ensures a continuous survey of the area for preventing all forms of human and animal pressure. Protected areas are set enclosure for 3 to 4 years and then are reopened to grazing activity (Amghar et al. 2012). The enclosed areas covered a total area of about

20.000 ha and the freely grazed steppes followed a year-round, continuous pattern of free grazing, with 5 sheep unit ha^{-1}, representing the traditional grazing regime for local pastoralists.

Climatic conditions

To assess the climatic conditions of the study site we analyzed and compared the drought severity during the period in which reliable monthly weather data were available (1988–2014). Weather data (mainly monthly-precipitation and -mean temperature) were obtained from the nearest weather station Bou-saâda (35.31°N, 3.90°E, elevation = 800 m a.s.l.). To measure drought severity, we applied a widely used drought index (the Standardized Precipitation-Evapotranspiration Index, SPEI; Beguería et al. 2014, Vicente-serrano et al. 2010) which is based on the climatic balance between precipitation and the atmospheric evaporative demand. SPEI incorporates both the multi-scalar character of the standardized precipitation index (SPI) and the evaporation component of the Palmer drought severity index (PDSI) and is better for drought assessment especially in semi-arid and arid regions (Vicente-serrano et al. 2010, Vicente-serrano et al. 2013, Beguería et al. 2014). Different SPEIs were obtained for different time-scales representing the cumulative water balance over the previous *n* months. Time scales of one, three, six and twelve months were used in this study to compute SPEI-1, SPEI-3, SPEI-6 and SPEI-12, respectively.

Sampling method of vegetation

We conducted a multi-site survey during the period of peak growth (late April-early May) in 2014. We selected five homogeneous sites in enclosed areas and another five in freely grazed areas. Within each site, three 200-m linear transects (30 transects in total) were carried out. Plant abundance and richness within each transect were estimated using the Point-Intercept Method (Goodall 1952), which consists of recording, at every 20-cm intervals, the identity of all individuals that are in contact with a vertical nail (Kouba et al. 2015). The abundance of each species in each transect was estimated from the number of individuals recorded along the same transect. Those plants that could not be identified with certainty in the field were brought to the laboratory for identification by botanists. Individual plants were collected with flowers or fruits as these characteristics are vital for identification. Voucher specimens of the collected plant species are available at the Centre of Scientific and Technical Research on Arid Regions (Biskra, Algeria). Plant nomenclature followed (Quézel and Santa 1962, Quézel and Santa 1963) and the International Plant Names Index (https://www.ipni.org/).

Data analysis

All analyses were performed using the statistical software R (R Core Team 2019).

Individual- and Indicator-species analysis

All species were classified in 12 categories according to their response to management type (Hanke et al. 2014, Garnier et al. 2018) and Dominant-Subordinate-Transient (DST) classification (Whittaker 1965). Species response types comprised (1) loss, species that exclusively occur in the grazed steppes; (2) colonizer, species that occur exclusively in the grazing-excluded steppes; (3) decreaser, species with significantly lower abundance in the grazing-excluded steppes; (4) increaser, species with significantly higher abundance in the grazing-excluded steppes, and (5) stable, species with no significant change in abundance. It should be noted that assignments were based on the comparison of abundances of each plant species between the two management types (grazed vs. grazing-excluded) using the non-parametric Mann–Whitney U test at a significance level of 0.05. For DST classification, we followed (Mariotte 2014): species with a cumulative relative abundance below 2% were considered as transients (T), comprised between 2% and 12% as subordinates (S) and >12% as dominants (D).

Indicator species analysis was used to assess the strength of the association between plant species and management type. This analysis is based on both, species fidelity which is the relative frequency of species within-group (i.e. the number of sample units in which the species occurs, within the same group) and exclusivity which reflects the concentration of species abundance within a particular group (Cáceres et al. 2012) . Ideal indicator species is so exclusively faithful to a group (grazed or grazing-excluded steppes) and occurs in all transects within a steppe type. The Indicator species analysis was performed using the function *multipart* of the package "indicspecies".

Alpha and functional groups diversities analysis

The recorded plant species were classified into functional groups based on these functional traits: growth forms (shrubs, forbs, graminoids), life span (annuals, perennials) and Raunkiaer life-forms (therophytes, chamaephytes, hemicryptophytes, geophytes). Gower's similarity coefficient among species was calculated using *gowdis* function. The resulted Gower's similarity matrix was then introduced into a clustering analysis with Ward method using *hclust* function of "cluster" package. Cluster classification led to the definition of six functional groups differing mostly by growth forms and Raunkiaer life-forms (Appendix S1). Species in functional group 1 (hereafter, FG1) were therophytic annual forbs, second functional group (hereafter, FG2) included hemicryptophytic perennial forbs, third functional group (hereafter, FG3) consisted of therophytic annual graminoids, forth functional group (hereafter, FG4) consisted of hemicryptophytic perennial graminoids, fifth functional group (hereafter, FG5) included chamaephytes, and sixth functional group (hereafter, FG6) comprised geophytes. The latter group contained only three species then was removed from the analysis of alpha diversity.

The diversity of each functional group in each transect was quantified using Hill Numbers (^{q}D) (Chao et al. 2014). The *q*-metric of Hill index reflects the sensitivity of the index to relative abundances of species; here the following *q* values were used: (i) $q = 0$ which reflects species richness, (ii) $q = 1$ is equivalent to the exponential of Shannon's entropy index (great weight is given to common species), and (iii) $q = 2$ is the equivalent of the inverse of Simpson's concentration index (great weight is given to dominant species).

The effect of the current management (grazed *vs.* grazing-excluded) on alpha diversities was analyzed using generalized linear mixed models (GLMM) with the *glmer* function in package "lme4". The management was entered as a fixed factor and the site was added as a random factor to control for site-level effects. Moreover, the strengths of the relationships between alpha diversity measures of all functional groups were tested separately in grazed and grazing-excluded steppes using Pearson correlation tests.

Beta diversity analysis

To quantify community dissimilarity, we used multiple-sites incidence-based and abundance-based dissimilarities proposed by Baselga (Baselga 2010, Baselga 2013, Baselga 2017). Multiple-site incidence-based dissimilarity based only on species identities and additively partition overall beta diversity to spatial turnover (i.e. species replacement independent of species richness gradients) and nestedness-resultant (i.e. dissimilarity due solely to species richness differences) components (Baselga 2010). Whereas, multiple-site abundance-based dissimilarity account for variation in species composition in terms of species abundances and occurrences and separates the components of the overall beta diversity caused (i) by balanced variation in abundance (i.e. the substitution of the individuals of some species by the same numbers of individuals of different species in other sites; Baselga 2013) and (ii) abundance gradients (i.e. one assemblage is a subset of another; Baselga 2013). We followed the same notation as Baselga (Baselga 2010, Baselga 2013, Baselga 2017) using Sørensen dissimilarity (β_{SOR}) as a measure of incidence-based beta diversity and its two components: turnover measured as Simpson dissimilarity (β_{SIM}) and nestedness, measured as nestedness-resultant fraction of Sørensen dissimilarity (β_{SNE}), [$\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$]. Similarly, Bray–Curtis dissimilarity was used as a measure of abundance-based beta diversity (β_{BRAY}) and its two components: balanced variation ($\beta_{BRAY.BAL}$) and abundance gradients ($\beta_{BRAY.GRA}$), [$\beta_{BRAY} = \beta_{BRAY.BAL} + \beta_{BRAY.GRA}$].

Measures of beta diversity were calculated at two spatial levels. Transect-level (grain = transect and extent = site), at this level multiple-site dissimilarity measures reflect within sites variations (i.e. local variation in species composition). Site-level (grain = site and extent = grazing management type{grazed/grazing-excluded}), at this level multiple-site dissimilarity measures reflect among sites within management type variation. Beta diversity analysis was performed using the functions *beta.sample* and *beta.sample.abund* in package “betapart”. Multiple-site dissimilarities were computed 100 times for randomly sampled subsets of 2 sites.

We analyzed the effect of the management type on multiple-site β-diversities at (1) transect level, using GLMM (function *glmer* from package “lme4”), with the management type as a fixed factor and the site as a random factor, (2) site level by using GLM (function *glm* from package “stats”) with management type as a fixed factor. Variations of multiple-site β-diversities between the two spatial levels in each grazing management type were also analyzed using GLMs. For both GLMM and GLM, we followed different error distributions (e.g. Gaussian, gamma, Poisson) depending on the nature of errors.

RESULTS

Temporal variation of drought

Overall, SPEIs showed complex variations from 1988 to 2014, with a significant decreasing trend ($p < 0.001$) of 0.025/yr, 0.037/yr, 0.055/yr, and 0.065/yr for 1-, 3-, 6- and 12-month SPEI, respectively (Fig. 2). The decreasing rate increased with time-scale; that is, long SPEI time-scales decreased more than short SPEI time-scales, reflecting the increasing severity of long time-scales drought. SPEI-6 and SPEI-12 revealed a long episode of drought (SPEI < 0) between May 2012 and December 2014 (Fig. 2). Furthermore, the month of April in 2014 (the period during which vegetation was sampled) was severely dry (values of SPEI-1, SPEI-3, SPEI-6 and SPEI-12 were -2,18, -1,40, -1,39, and -1,17, respectively).

Individual- and Indicator-species

In total we recorded 100 plant species among them 93 species occurred in the grazing-excluded steppes (85 transients, 6 subordinates, and 2 dominant species) and 60 species occurred in grazed steppes (49 transients, 10 subordinate, and 1 dominant species) (Table 1). The individual species analysis (Fig. 3, Appendix S1) revealed a high number of colonizers (40 species) followed by increasers (27 species) and most of them (70% and 66.7% of colonizers and increasers, respectively) were therophytes. Furthermore, *H. salicifolium* and *A. cyrtolepidioides* have increased their abundances in the exclosures to become subordinate and dominant species, respectively. In addition, these two species were selected as indicators of grazing-excluded steppes (see below).

Individual species analysis showed also that all the losses (7 species) were transient species and among the decreasers (13 species), four species (namely: *Koeleria pubescens*, *Micropus bombycinus*, *Noaea mucronata*, *S. lagascae*) were converted from being subordinate species in grazed steppes to become transient species in grazing-excluded steppes (Appendix S1). Furthermore, among stable species (13 species) there were one dominant species *S. tenacissima* and two subordinate species *Filago spathulata* and *Malva aegyptiaca*. This observation, in particular, means that the abundance of the most dominant species *S. tenacissima* did not increase significantly in the exclosures.

Indicators species analysis selected 14 significant ($p \leq 0.05$) indicator species and most (13 species) of them were indicative of grazing-excluded steppes; only one species "*Schismus barbatus*: therophytic annual graminoid" that was indicative of grazed steppes and was categorized as decreaser (Table 2). Among the species that were indicative of grazing-excluded steppes, three were categorized as colonizers and ten as increasers and most of these indicator species were therophytes and typical to Mediterranean steppes (Table 2). Furthermore, three of the selected indicator species were endemic species and seven were psammophytes (Table 2).

Alpha and functional groups diversities

When all species were introduced in the analysis, Hill index (with $q = 0$ or $q = 1$) was significantly greater in grazing-excluded than grazed steppes (Fig. 4 p, q); that is, the overall richness and the number of common species was bigger in grazing-excluded steppes. Regarding functional groups, only FG1 and FG3 were shown statistically significant differences between the two management types. In the case of FG1, Hill index (with $q = 0$ or $q = 1$) was significantly higher in grazing-excluded steppes (Fig. 4 m, n). Regarding FG3, Hill index was also significantly higher in grazing-excluded steppes for $q =$ 01or $q = 2$ (Fig. 4 h, i). The above means that short-term grazing exclusion increased significantly the number of common and dominant annual therophytic species (either forbs or graminoids).

Correlation analyses among diversity metrics of functional groups revealed significant negative associations between the diversity metric (Hill index with $q = 0$) of FG4 and that of FG5 (Hill index with $q =1$ or $q = 2$). Besides, the abundance of *S. tenacissima* was significantly positively associated with the diversity metrics of FG3 (Fig. 5a). Regarding grazd steppes, correlation analyses showed significant positive correlations between the diversity metrics of FG1 and FG3, and between those of FG2 and FG4 in the grazed steppes (Fig. 5b). In addition, the abundance of *S. tenacissima* was significantly negatively associated with the diversity metrics of FG2 (Hill index with $q = 0$) and FG4 (Hill index with $q = 0$ or $q = 1$).

Beta diversity

Abundance-based beta diversity measures

Both β_{BRAY} and $\beta_{\mathrm{BRAY.BAL}}$ were significantly higher in grazing-excluded steppes compared to grazed ones at site level (Fig. 6a, e) and the contrary occurred at transect level (Fig. 6b, f), while they were significantly higher at the site than at the transect level in grazing-excluded steppes (Fig. 6d, h). Nevertheless, these two measures did not differ significantly between the two spatial levels in grazed steppes. $\beta_{\mathrm{BRAY.GRA}}$ was significantly superior in grazed steppes at the site level (Fig. 6i) and at transect level in grazing-excluded steppes (Fig. 6l). Furthermore, this measure did not differ significantly between the two management types at the transect level, and between the two spatial levels in grazed steppes.

Incidence-based beta diversity measures

β_{SOR} was significantly higher in grazed steppes at the site level (Fig. 6m) but did not differ significantly between the two management types at the transect. Similarly, this measure of beta diversity did not differ significantly between spatial levels in both management types. β_{SIM} was significantly superior, in grazed steppes at the site level (Fig. 6q), and at site level in grazed steppes

(Fig. 6s). β_{SNE} was significantly higher in grazed steppes at transect level (Fig. 6v), and at transect level in grazed steppes (Fig. 6w).

Comparison between abundance-based and incidence-based beta diversity measures

β_{BRAY} and β_{SOR} were largely due to the increasing values of $\beta_{\mathrm{BRAY.BAL}}$ and its analogous β_{SIM}, respectively. The contribution of either $\beta_{\mathrm{BRAY.GRA}}$ or β_{SNE} to overall beta diversity was minor, did not exceed 14% in all cases. When compared between the two management types, β_{BRAY} and β_{SOR} and their components showed opposing results at the site level, but at transect level only β_{BRAY} that varied significantly. When compared between the two spatial levels, both β_{BRAY} and β_{SOR} did not differ significantly in grazed steppes, nevertheless in grazing-excluded steppes, β_{BRAY} and its components varied significantly.

DISCUSSION

Species-specific responses to sheep exclusion

In general, our findings showed that responses of plant communities to sheep grazing exclusion are partly species-specific. We found a high number of colonizers and increaser species in the exclosures which implies that grazing exclusion can offer appropriate habitats for the installation of new species (as a result of seed dispersal from the regional species pool) and for increasing the abundance of some existing species. The fact that a large portion of the colonizers and increasers were therophytes is probably related to climatic conditions (i.e., severe drought) which limit the reproduction of other life forms then therophytes that have a strategic adaptation to extreme climatic conditions (Bradai et al. 2015). In particular, our analysis pointed out two important increasers *H. salicifolium* and *A. cyrtolepidioides* which in addition of increasing their abundance, these two species were selected as indicators of grazing-excluded steppes. Essentially, *A. cyrtolepidioides* become dominant species, along with *S. tenacissima*, in sites protected from grazing, which will undoubtedly allow it to play an important role in structuring plant communities and the ecosystem functioning. Overall, this finding supports the idea that short-term exclusion induces shifts in plant species dominance in less productive environments. Our analysis revealed also that all the losses were transient species which were probably absent in the excclosures due to competitive exclusion and/or severe drought.

The increasing number of native indicator species in the exclosures compared to grazed steppes suggests the occurrence of important environmental changes. It seems that the protection of Alfa steppes from sheep grazing allows the recovery of steppe-native species and particularly some palatable and endemic species which reflects the importance of grazing exclusion for biodiversity restoration in arid regions. However, the fact that a great portion of exclosure-indicator species were psammophytes reflects sand accumulation on the soil surface which implies the commencement of land degradation process (Slimani et al. 2010, Amghar et al. 2012). A similar finding was reported by Slimani et al. (2010) who found sand encroachment within the exclosures and attributed this to additional sand inputs coming from neighboring degraded steppes as a result of wind-based erosion. Amghar et al. (2012) suggested that the optimum period for grazing exclusion is 3-4 years, beyond this threshold starts the loss of biodiversity due to competitive exclusion between plants and the establishment of dry crust on the ground due to the long absence of livestock trampling, as well as the accumulation of sand from degraded steppes through Aeolian erosion. In our opinion, one solution to avoid sand accumulation in protected areas is the application of appropriate sheep stocking rates in the surrounding steppes to prevent them from further degradations.

Effects of sheep exclusion on overall alpha diversities and functional groups' diversities

Overall, our study revealed a clear effect of short-term grazing exclusion, under severe drought episode, on plant community diversity in Alfa steppe rangelands with a long-term sheep grazing. Mainly, the results showed that short-term grazing exclusion had positive effects on the size of the regional species pool (i.e., the total number of species) and α-diversities (i.e., overall richness and total number of common species). These results are consistent with the widely admitted effect of grazing exclusion on species diversity in low-productivity systems (Deléglise et al. 2011). Overall, such rapid recovery of the vegetation diversity is common in North African steppes that have evolved under a long history of grazing and highlights the high resilience of this ecosystem to perturbations (Golodets et al. 2011). Le Houérou (1995) stressed that the vegetation in these arid regions has adapted to recurrent drought conditions over centuries and past millennia acquiring an ability to recover their characteristics after disturbance. Similarly, Tang et al. (2016) suggested that livestock exclusion can safeguards rangeland from livestock-induced disturbances and accelerate the recovery of degraded pasture species.

The enhancement of the overall α-diversity observed in this study is mainly attributed to the significant increases in diversity scores of the two dominant plant functional groups (PFGs), therophytic-forbs (FG1) and therophytic-graminoids (FG3) in exclosures, as other functional groups did not increase significantly. This supports the notion that the responses of PFGs to short-term grazing exclusion under severe drought episodes are identity-dependent (Liang et al. 2018).

Several authors have considered therophytization as a characteristic of arid steppes and drylands, as it is a strategy of ecosystem adaptation to extreme climatic conditions (Jauffret and Lavorel 2003, Neffar et al. 2018). Therophytes are more resistant to summer drought than hemicryptophytes and geophytes because their life cycle is adapted to the seasonal stress (highly stress-tolerant) (Madon and

Médail 1997, Jauffret and Lavorel 2003). Therophytes avoid drought by seasonal dormancy: they complete their life cycle only in one season by reproducing just before the arrival of the dry season and remain in the soil as dormant seeds (Gao et al. 2015, Neffar et al. 2018). On the other hand, they are considered as species with r-strategy (Madon and Médail 1997) which enables them to extend their populations speedily. Overall, the short life-span together with a good production of seeds per individual and weak mortality are the characteristics that allow this functional group to spread rapidly (Madon and Médail 1997) and thus increase its diversity. Furthermore, it has been argued that sand encroachment in exclosures can form a dry crust that stops evaporation and maintains a certain water moisture in the soil "self-mulching" and thus promotes the development of therophytes (Amghar et al. 2012, Amghar et al. 2016).

Short-term grazing exclusion did not enhance the diversities of FG2, FG4 and FG5, which is likely due to severe drought (i.e. these functional groups are strongly depending on precipitation). This finding reveals that short-term grazing exclusion becomes benefic for these functional groups only when it is applied during periods with favorable climatic conditions, mainly with sufficient precipitation amount (Kakinuma et al. 2017).

Free grazing under severe drought altered the relationships among the PFGs. Specifically, our results suggested a positive correlation between the diversities of FG1 and FG3 and between FG2 and FG4 however such positive feedbacks between PFGs disappeared in the exclosures. This finding supports the notion that plant species and PFGs can have strong interactions, i.e. facilitation, under high physical stress (e.g. severe drought) and in communities with high consumer pressure (e.g. high livestock grazing pressure) (Maestre and Puche 2009, Pueyo et al. 2009, Liang et al. 2018). The observed negative correlations between species richness of FG4 and the number of common and dominate species of FG5 in the exclosures reflect the dominance of competitive interactions between these two PFGs in the absence of herbivory and as a result of niche overlap (Liu et al. 2019). Furthermore, the positive correlation between the abundance of *S. tenacissima* and FG3 diversity in the exclosures reflects facilitation interactions between this nurse species and therophytic graminoids. *S. tenacissima* tussock creates suitable microclimatic conditions for the installation of new individuals and new species and some species such as *Centaurea incana* and *Dactylis glomerata* only grow within the tufts; which makes *S. tenacissima* a keystone species, upon which the functioning of the entire ecosystem relies on (Slimani et al. 2010, Lahniar-Zemiti and Aidoud 2016).

Effects of sheep exclusion on β-diversities at local and regional scale

The significant responses of incidence- and abundance-based β-diversity to protection from grazing at both transect and site levels reveal that the effects of grazing exclusion under severe drought on plant community composition are expressed at small local scale as well as at broad landscape scale.

At the local scale, short-term sheep exclusion has decreased the overall abundance-based β-diversity, which was mainly driven by the balanced variation fraction, and the nestedness-resultant fraction (community subsetting) of the incidence-based β-diversity. The negative effect of sheep exclusion on the balanced variation in species abundance at a local scale can be explained by the increasing variation in species abundance. That is, some species have increased in abundance whereas others have decreased, which can be due to deterministic processes, i.e., the increasing competition for resources after a release from sheep grazing. Furthermore, the observed decline in community subsetting, which is caused mainly by environmental gradient (Ulrich et al. 2009), indicates that nested communities have increased their richness after the vanishing of sheep-induced disturbances probably as a result of stochastic processes, i.e., increasing dispersal from a regional species pool (as we have seen above there were 40 colonizers) which augmented in size in the exclosures. This is consistent with the increase in mean richness at the transect level witnessed in the exclosures. Overall, this finding is in line with other studies that reported that the exclusion of livestock grazing can alter species composition and competitive relationships within plant communities (Jing et al. 2013, Wang et al. 2018*b*). Conversely, other studies have confirmed the role of grazing in the enhancement of fine-scale variability of species composition by increasing fine-scale environmental heterogeneity through selective grazing [sheep, in particular, are more selective than other herbivores (Tóth et al. 2018)], trampling, deposition of excreta, and by acting as dispersal agents (Limb et al. 2018, Wang et al. 2018*a*).

Whilst it is widely recognized that increased grazing leads to plant community homogenization at the landscape scale (Austrheim and Eriksson 2001) and thus grazing exclusion may undoubtedly increase the spatial variation in species assemblages; our results indicated that under severe drought the release from sheep grazing affected contrastingly the incidence- and abundance-base β-diversity. Sheep exclusion has increased the abundance-based β-diversity and its balanced variation fraction nevertheless has reduced the incidence-based β-diversity and its turnover component at the landscape scale (i.e. among sites). On the one hand, this finding can be explained by the increasing abundance of the dominant species *S. tenacissima* in the exclosures (although this increase was not significant) which likely affected species sorting by decreasing environmental heterogeneity at the landscape scale and hence decreased species turnover among sites. In addition, the severe drought may negatively affected species turnover (Tang et al. 2018) by causing the disappearance of some transient species from some sites (as we have seen above 7 transient species were lost). On the other hand, resources availability (litter accumulation) and facilitation interactions from *S. tenacissima* might have increased the abundance of less frequent species (we have found that 27 transient species were increased in abundance) at the landscape scale in the exclosures which both improved the balanced variation in abundance and reduced the abundance-gradient.

Protection from grazing has affected β-diversities scaling patterns, mainly has led to a significant spatial structuration of abundance-based β-diversities and the loss of the spatial structuration of incidence-based β-diversities (i.e. did not vary significantly between spatial levels). Particularly, abundance-based β-diversity and its balanced variation fraction were bigger at the landscape scale (i.e. among sites) following grazing exclusion, whereas its abundance-gradient fraction was higher at the local scale (i.e. among transects). This reflects that short-term grazing exclusion maintains higher balanced variation in species abundance at large spatial scale and greater abundance-gradient in species composition at the fine-scale. This can be due to the increased facilitation interactions from *S. tenacissima* at the landscape level and amplified deterministic processes such as competition at the local scale in the exclosures. This finding is partially consistent with the study of (Deléglise et al. 2011) which found a positive relationship between spatial variability of species composition and grain size in grazing excluded areas.

CONCLUSIONS

Our study provides insights into the effects of short-term sheep grazing exclusion under severe drought episodes, on individual plant species, diversities of PFGs, α- and β-diversity components in the North African Alfa steppes. The results point out the importance of short-term sheep exclusion in improving the regional plant species pool and α-diversities (i.e., overall richness and the total number of common species). Furthermore, this management practice allowed the colonization of many new species and the recovery of some palatable and endemic steppe-native species which reflects its importance for biodiversity restoration in hot arid regions, particularly during prolonged droughts.

However, because of the severe drought, the enhancement of the overall α-diversity was mainly due to the significant increase of diversity of therophytes (either forbs or graminoids) which represent an adaptive strategy to adverse conditions and a form of resistance to severe droughts. These findings support the notion that the responses of PFGs to short-term exclusion under severe drought episodes are identity-dependent. Short-term sheep grazing exclusion altered the relationships between PFGs by creating competitive interactions between FG4 and FG5 and facilitation interactions between *S. tenacissima* and FG3. Last but not least, our study revealed that the effects of sheep exclusion under severe drought on plant community composition are expressed at local scale as well as at landscape scale. Essentially, short-term exclusion maintains higher balanced variation in species abundance at a large spatial scale and greater abundance-gradient in species composition at the fine-scale.

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TABLE 1. Characteristics of the sampled Alfa-steppes. Some values are mean ± standard deviation.

Steppe characteristics	Grazing-excluded steppes	Grazed steppes	Overall
Altitude a.s.l. (m)	826.33±113.20	857.67±71.35	842±94.33
Slope (°)	3.89±1.97	3.42±1.82	3.66±1.88
Number of transects	15 (3 per site)	15 (3per site)	30
Number of sampled sites	05	05	10
Total number of sampled individuals	12020	8916	20936
Number of sampled individuals per transect	801.33±186.37*	594.40±100.57*	697.87±180.90
Distance among transects within the same site (m)	273.62±123.05	263.61±156.11	267.36±141.86
Distance among sites (km)	16.55±7.74	30.66±16.87	23.60±14.80
Total number of sampled species	93 (85, 6, 2)**	60 (49, 10, 1)**	100
Vegetation cover (%) per transect	57.51±9.00*	38.19±9.94*	47.85±13.54

* means that the difference between the two management types was statistically significant ($p \leq 0.05$) based on paired t test.
** figures between parentheses are numbers of transient, subordinate, and dominant species, respectively.

TABLE 2. Indicator species associated with either grazed or grazing-excluded Alfa steppes and their characteristics.

Species	IV[a]	MT[b]	PFGs[c]	SC[d]	PAL[e]	EG[f]	Phytochory[g]	Endemism
Anacyclus cyrtolepidioides	0.898	UG	FG1	SDI	HP	Psammophyte	MS	North Africa
Scorzonera undulata	0.894	UG	FG1	TC	HP	Psammophyte	MS	North Africa
Helianthemum salicifolium	0.847	UG	FG1	TSI	MP	Silty-clay soils	MS	—
Aizoon hispanicum	0.837	UG	FG1	TTI	UP	Halophyte	MS	—
Eruca vesicaria	0.832	UG	FG1	TTI	MP	Silty soils	Med	—
Herniaria fruticosa	0.805	UG	FG2	TTI	MP	Gypsophyte	MS	North Africa
Scabiosa stellata	0.801	UG	FG3	TTI	MP	Psammophyte	Med	—
Schismus barbatus	0.794	G	FG3	TTD	HP	Psammophyte	MS	—
Euphorbia falcata	0.776	UG	FG1	TTI	UP	Silty-clay soils	Med	—
Launaea resedifolia	0.758	UG	FG1	TTI	HP	Psammo-halophyte	MS	—
Erodium triangulare	0.746	UG	FG1	TTI	MP	Psammophyte	MS	—
Iris sisyrinchium	0.693	UG	FG6	TTI	UP	Silty soils	MS	—
Lithospermum apulum	0.683	UG	FG1	TC	UP	Sandy-clay soils	MS	—
Astragalus cruciatus	0.577	UG	FG1	TC	HP	Psammophyte	Med	—

[a] Indicator Value (only species with significant “$p \leq 0.05$” indicator values were retained).

[b] Management type which includes grazed (G) and ungrazed (UG) Alfa-steppes

[c] Plant functional groups: FG1, therophytic annual forbs; FG2, hemicryptophytic perennial forbs; FG3, therophytic annual graminoids; FG6, Geophytes.

[d] Species categories: TTI, transient-transient increaser; TTD, transient-transient decreaser; TSI, transient-subordinate increaser; TC, transient colonizer; SDI, subordinate-dominant increaser (the first and second letters refer to DST classification in grazed and ungrazed steppes successively whereas the third letter refers to species response type).

[e] Palatability: HP, highly palatable; MP, moderately palatable; UP, unpalatable.

[f] Edaphic group/conditions of each plant species

[g] Phytochory (Le Houérou 1995): MS, Mediterraneo-steppic; Med, Mediterranean *sensu lato*

FIGURES LEGENDS

FIG. 1. Geographical settings of the study are. (a) location of the study area in the steppe rangelands of Algeria, black solid points (●) indicate locations of sampled sites in grazed steppes and white solid points (○) represent locations of sampled sites in grazing-excluded steppes. (b) and (c) photographs taken in grazing-excluded and grazed steppes successively.

FIG. 2. Evolution of the SPEI between 1988 and 2014 at the steppe rangelands of central Algeria. SPEI-1, SPEI-3, SPEI-6, and SPEI-12 refer to 1-, 3-, 6- and -12-month SPEI, respectively. Red color reflects episodes of drought and bleu reflects wet episodes.

FIG. 3. Species categorization based on species-specific response to management type and DST classification. The first and the second letters of each category refer to DST classification (i.e. dominant, subordinate, transient) in grazed and grazing-excluded steppes, respectively; the third letter refers to species response type (i.e. increaser, decreaser, stable, colonizer, loss). TC, transient colonizer; TTI, transient-transient increaser; TTS, transient-transient stable; TTD, transient-transient decreaser; TL, transient loss; STD, subordinate-transient decreaser; SSI, subordinate-subordinate increaser; SSS, subordinate-subordinate stable; DDS, dominant-dominant stable; SDI, subordinate-dominant increaser; SSD, subordinate- subordinate decreaser; TSI, transient-subordinate increaser.

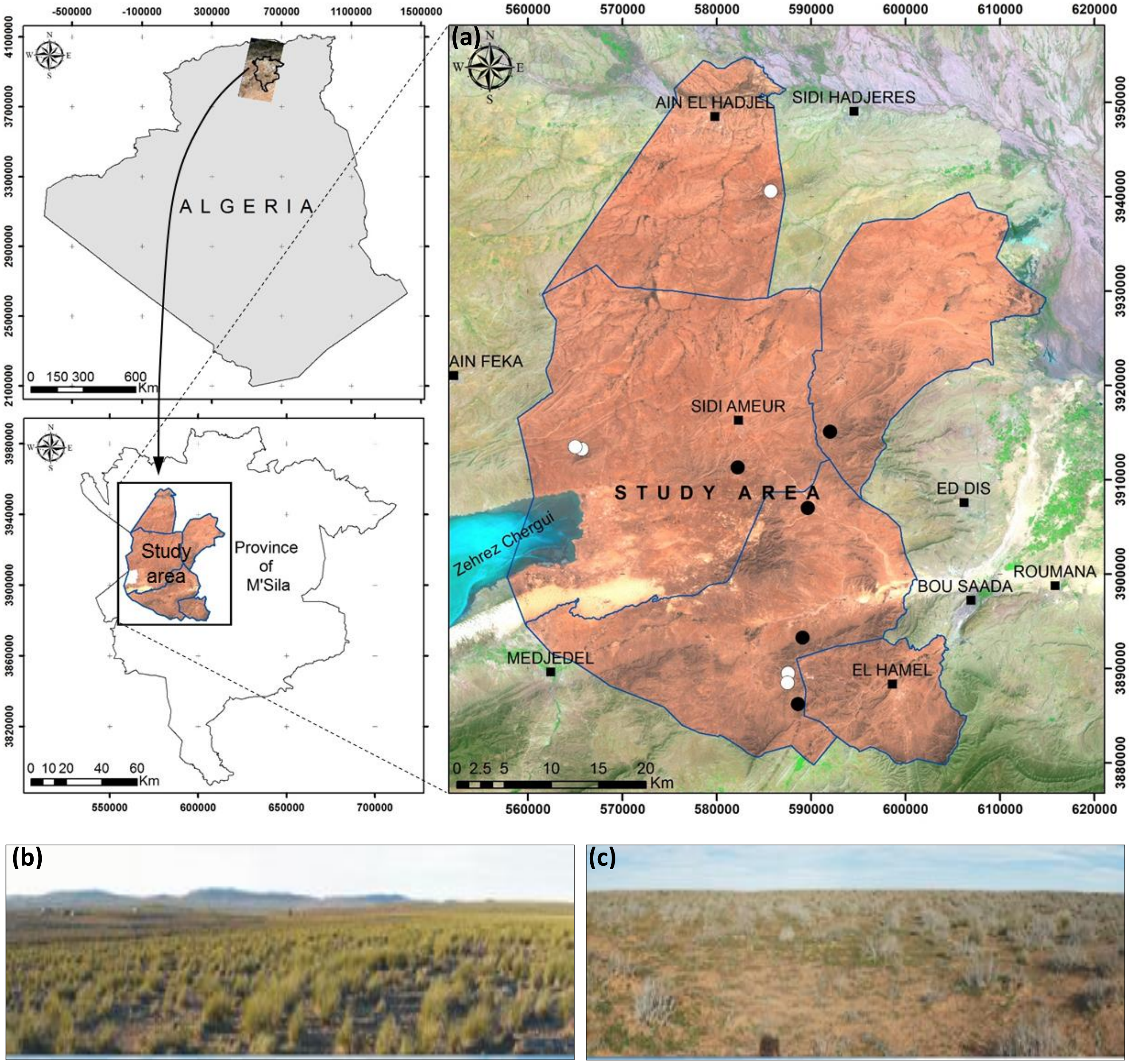
FIG. 4. Pirate plots comparing Hill Numbers (^{q}D) diversities for each trait-based plant functional group between grazed and grazing-excluded steppes in arid rangelands of Algeria. AS: all plant species included, FG1: therophytic annual forbs, FG2: hemicryptophytic perennial forbs, FG3: therophytic annual graminoids, FG4: hemicryptophytic perennial graminoids, FG5: chamaephytes. Results of GLMM are also shown (***, **, *, ^{ns} are significance levels at 0.001, 0.01, 0.5, and not significant, respectively).

FIG. 5. Spearman correlations between alpha diversity measures of plant functional groups (i.e. Hill Numbers (^{q}D) with q=0, q=1, or q=2) as well as the abundance of the dominant species (*Stipa tenacissima*) in grazing-excluded (a) and grazed (b) steppes. FG1, therophytic annual forbs; FG2, hemicryptophytic perennial forbs; FG3, therophytic annual graminoids; FG4, hemicryptophytic

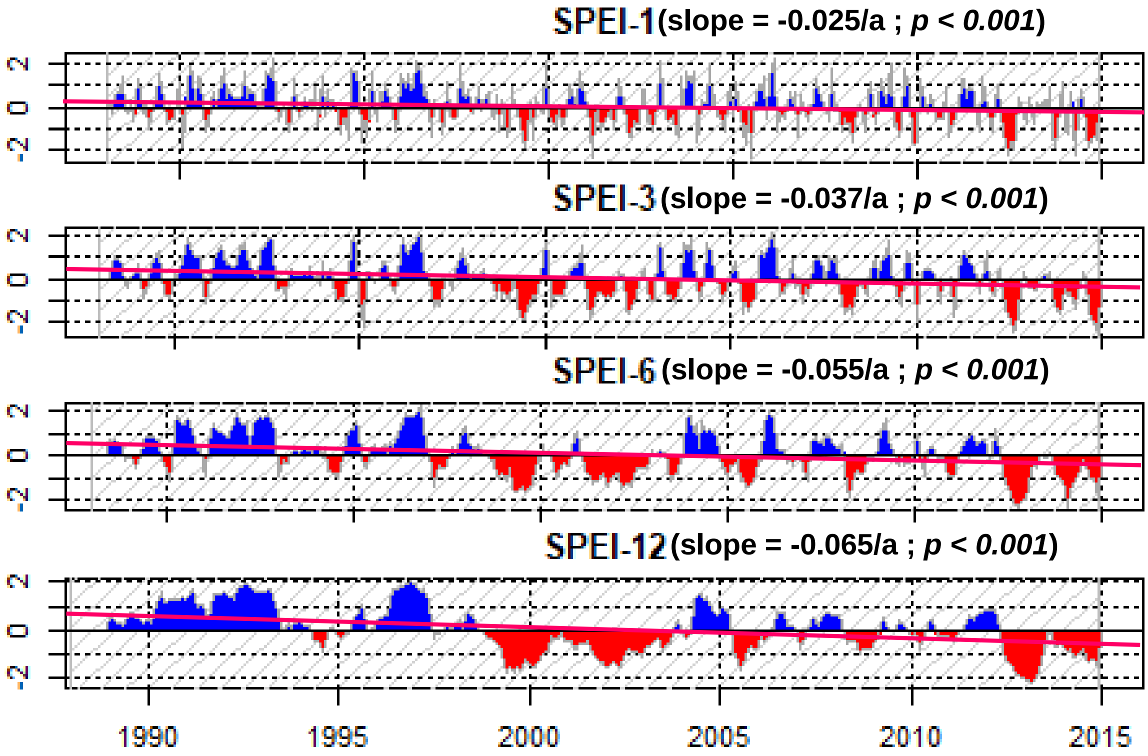
perennial graminoids; FG5, chamaephytes. Correlation coefficients are shown by color and intensity of shading in squares. (*, **, ***) are significance levels at 0.05, 0.01, 0.001, respectively.

FG. 6. Comparison of beta diversity measures between grazed and grazing-excluded steppes at two spatial levels (transect and site) and between the two spatial levels (transect vs. site) in both steppe types (grazed and grazing-excluded). β_{BRAY} is the overall abundance-based multi-site dissimilarity measured as Bray-Curtis multiple-site dissimilarity; $\beta_{\mathrm{BRAY.BAL}}$ is the balanced variation fraction of Bray-Curtis dissimilarity; $\beta_{\mathrm{BRAY.GRA}}$ is the abundance-gradient of Bray-Curtis dissimilarity. β_{SOR} represents the overall incidence-based multi-site beta diversity measured as Sørensen dissimilarity; β_{SIM} is the turnover component of Sørensen dissimilarity measured as Simpson dissimilarity; β_{SNE} is the nestedness-resultant fraction of Sørensen dissimilarity. (***, **, *, $^{\mathrm{ns}}$ are significance levels at 0.001, 0.01, 0.5, and not significant, respectively).

FIG. 1.


ALGERIA
Study area
Province of M'Sila
(a)
AIN EL HADJEL
SIDI HADJERES
AIN FEKA
SIDI AMEUR
STUDY AREA
ED DIS
Zehrez Chergui
BOU SAADA
ROUMANA
MEDJEDEL
EL HAMEL
0 2.5 5 10 15 20 Km
0 150 300 600 Km
0 10 20 40 60 Km
(b)
(c)

745 FIG. 2.



746

747

748

FIG. 3.

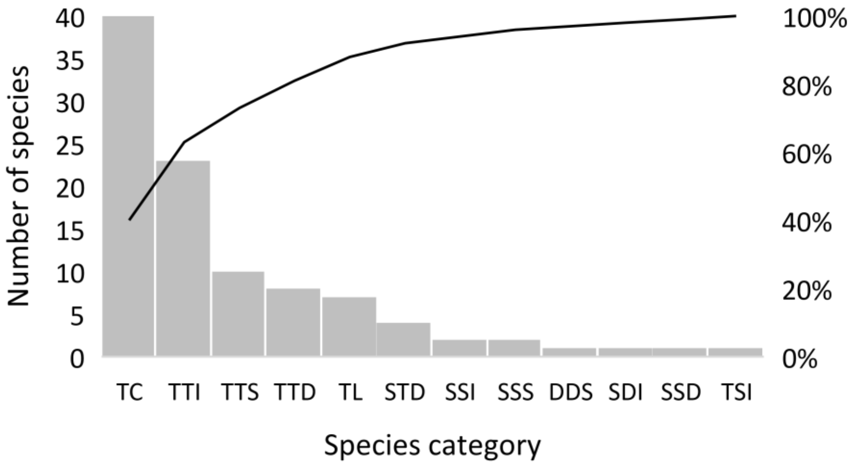

Number of species
40
35
30
25
20
15
10
5
0
100%
80%
60%
40%
20%
0%
TC
TTI
TTS
TTD
TL
STD
SSI
SSS
DDS
SDI
SSD
TSI
Species category

FIG. 4.

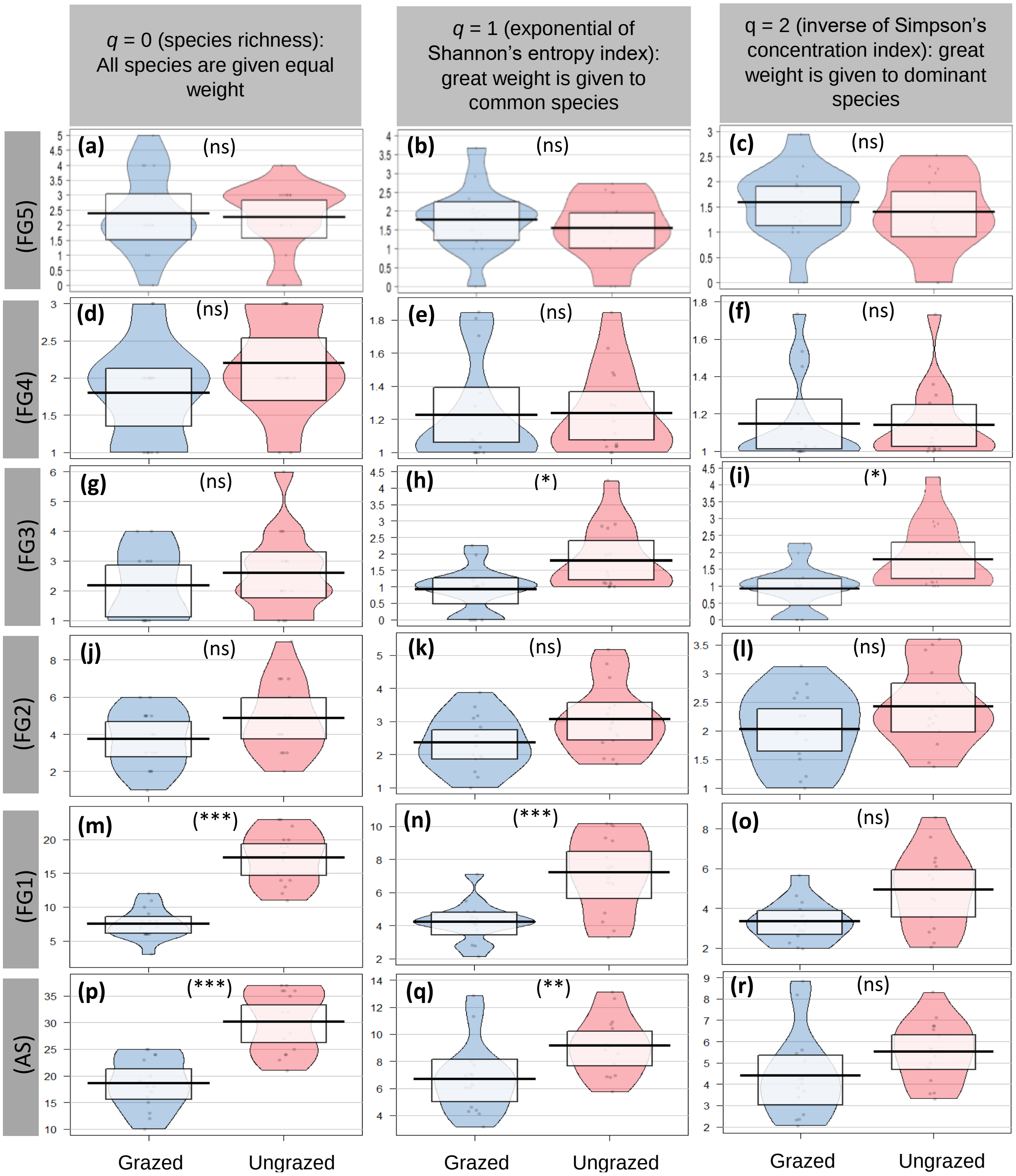

q = 0 (species richness): All species are given equal weight
q = 1 (exponential of Shannon's entropy index): great weight is given to common species
q = 2 (inverse of Simpson's concentration index): great weight is given to dominant species
(FG5)
(a) (ns)
(b) (ns)
(c) (ns)
(FG4)
(d) (ns)
(e) (ns)
(f) (ns)
(FG3)
(g) (ns)
(h) (*)
(i) (*)
(FG2)
(j) (ns)
(k) (ns)
(l) (ns)
(FG1)
(m) (***)
(n) (***)
(o) (ns)
(AS)
(p) (***)
(q) (**)
(r) (ns)
Grazed
Ungrazed
Grazed
Ungrazed
Grazed
Ungrazed

FIG. 5.

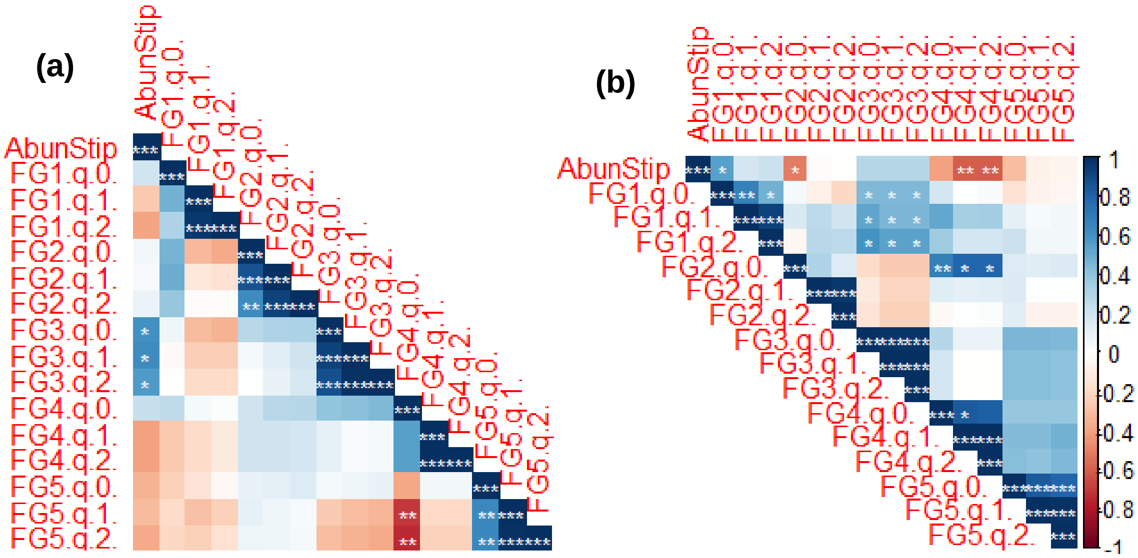
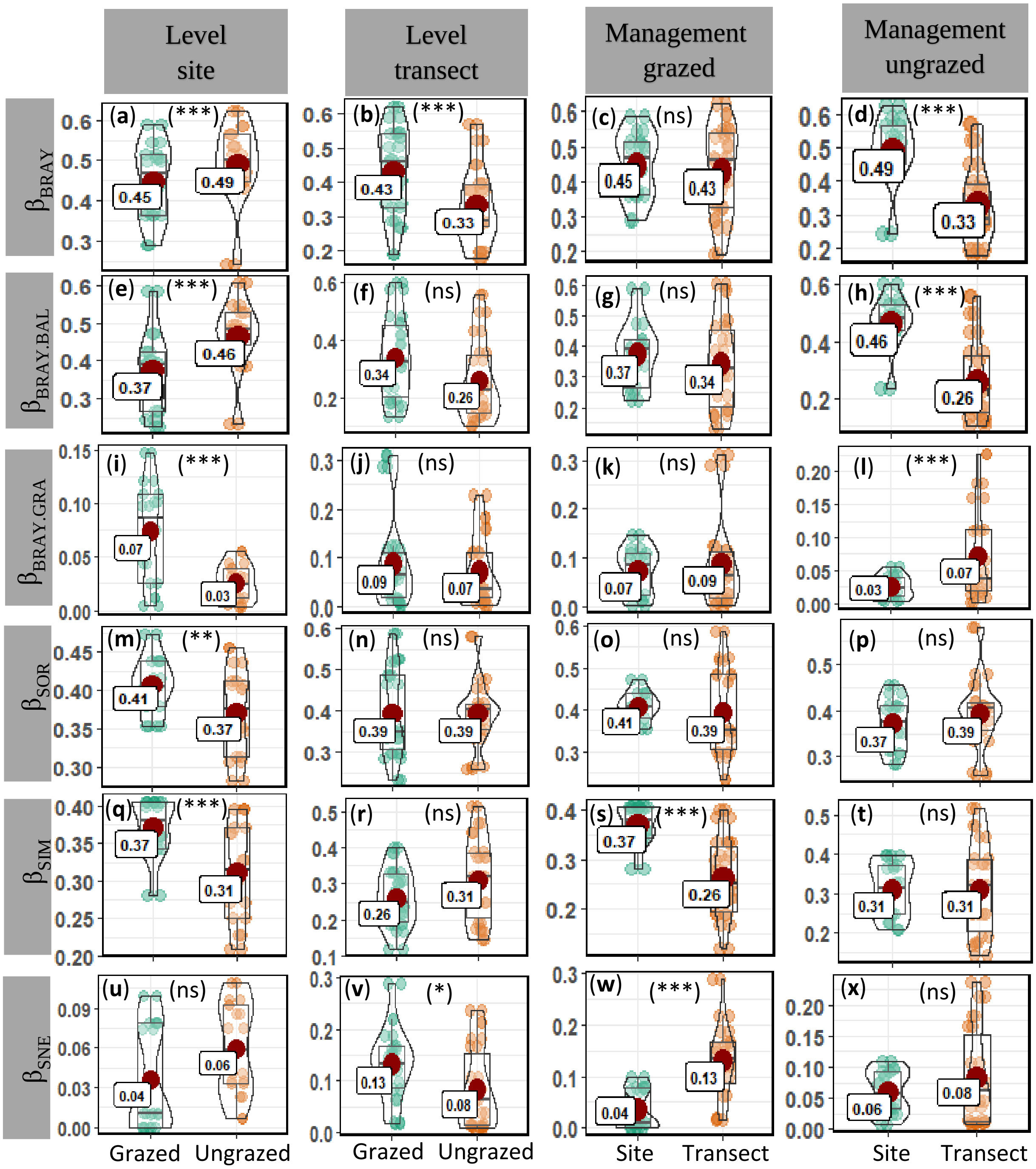

(a)
AbunStip
FG1.q.0.
FG1.q.1.
FG1.q.2.
FG2.q.0.
FG2.q.1.
FG2.q.2.
FG3.q.0.
FG3.q.1.
FG3.q.2.
FG4.q.0.
FG4.q.1.
FG4.q.2.
FG5.q.0.
FG5.q.1.
FG5.q.2.
(b)
AbunStip
FG1.q.0.
FG1.q.1.
FG1.q.2.
FG2.q.0.
FG2.q.1.
FG2.q.2.
FG3.q.0.
FG3.q.1.
FG3.q.2.
FG4.q.0.
FG4.q.1.
FG4.q.2.
FG5.q.0.
FG5.q.1.
FG5.q.2.
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

FIG. 6.


Level site
Level transect
Management grazed
Management ungrazed
βBRAY
βBRAY.BAL
βBRAY.GRA
βSOR
βSIM
βSNE
(a) (***) 0.45 0.49
(b) (***) 0.43 0.33
(c) (ns) 0.45 0.43
(d) (***) 0.49 0.33
(e) (***) 0.37 0.46
(f) (ns) 0.34 0.26
(g) (ns) 0.37 0.34
(h) (***) 0.46 0.26
(i) (***) 0.07 0.03
(j) (ns) 0.09 0.07
(k) (ns) 0.07 0.09
(l) (***) 0.03 0.07
(m) (**) 0.41 0.37
(n) (ns) 0.39 0.39
(o) (ns) 0.41 0.39
(p) (ns) 0.37 0.39
(q) (***) 0.37 0.31
(r) (ns) 0.26 0.31
(s) (***) 0.37 0.26
(t) (ns) 0.31 0.31
(u) (ns) 0.04 0.06
(v) (*) 0.13 0.08
(w) (***) 0.04 0.13
(x) (ns) 0.06 0.08
Grazed
Ungrazed
Grazed
Ungrazed
Site
Transect
Site
Transect

Appendix 1. Species-specific response to management type. PFGs, refers to plant functional groups and includes six groups (see the text for the names of groups); DST classification includes three classes, dominant (D), subordinate (S) and transient (S) species; Response types includes four categories, species that exclusively occur in the grazed steppes (loss), species that occur exclusively in the grazing-excluded steppes (colonizer), species with lower abundance in the grazing-excluded steppes (decreaser), species with higher abundance in the grazing-excluded steppes (increaser), and species with no significate change in abundance (stable). Assignments are based on the comparison of the abundance of each plant species between the two management types (grazed vs. grazing-excluded) using Mann–Whitney U test at a significance level of 0.05 (The significant changes are in bold). Species abundance in each management type refers to the mean of absolute abundance per transect ± standard error. Species category comprises 12 categories (see legend of Figure 3 for names of the categories).

Species	PFGs	Grazed steppes		Grazing-excluded steppes		Change	Response type	Species category
		DST	Abundance	DST	Abundance			
Adonis dentata Delile	FG1	—	—	T	0.20±0.14	**0.20**	Colonizer	TC
Aizoon hispanicum L.	FG1	T	0.13±0.09	T	2.87±0.74	**2.73**	Increaser	TTI
Allium cupani Raf.	FG6	T	0.40±0.16	T	1.00±0.45	**0.60**	Increaser	TTI
Alyssum parviflorum M.Bieb.	FG1	T	1.67±1.20	T	4.93±3.79	**3.27**	Increaser	TTI
Ammoides verticillata (Desf.) Briq.	FG1	—	—	T	0.60±0.41	**0.60**	Colonizer	TC
Anabasis articulata (Forssk.) Moq.	FG5	T	6.07±6.07	T	0.07±0.07	**060**	Decreaser	TTD
Anacyclus cyrtolepidioides Pomel	FG1	S	21.40±7.62	D	89.33±17.30	**67.93**	Increaser	SDI
Argyrolobium uniflorum (Decne.) Jaub. & Spach	FG2	T	0.33±0.13	T	0.07±0.07	**0.27**	Decreaser	TTD
Aristida plumosa L.	FG4	T	0.40±0.40	—	—	**0.40**	Loss	TL
Artemisia campestris L.	FG5	T	3.00±1.03	T	6.87±2.44	**3.87**	Increaser	TTI
Artemisia herba-alba Asso	FG5	T	17.33±7.83	T	36.40±16.66	**19.07**	Increaser	SSI
Asparagus albus L.	FG5	—	—	T	0.87±0.61	**0.87**	Colonizer	TC
Asteriscus pygmaeus (DC.) Coss. & Durieu	FG1	T	2.20±1.02	T	7.40±2.45	**5.20**	Increaser	TTI
Astragalus cruciatus Link	FG1	—	—	T	0.67±0.29	**0.67**	Colonizer	TC
Atractylis cancellata L.	FG1	T	0.60±0.40	T	1.20±0.58	0.60	Stable	TTS
Atractylis delicatula Batt. ex L.Chevall.	FG2	—	—	T	0.13±0.09	**0.13**	Colonizer	TC
Atractylis prolifera Boiss.	FG1	—	—	T	8.80±6.12	**8.80**	Colonizer	TC
Atractylis serratuloides Sieber ex Cass.	FG2	T	3.27±1.67	T	1.07±0.65	**2.20**	Decreaser	TTD
Avena barbata Pott ex Link	FG3	—	—	T	0.87±0.42	**0.87**	Colonizer	TC
Avena sterilis L.	FG3	—	—	T	0.60±0.53	**0.60**	Colonizer	TC
Brachypodium distachyon (L.) P.Beauv.	FG3	T	0.87±0.87	T	2.13±2.06	**1.27**	Increaser	TTI
Bromus rubens L.	FG3	T	0.07±0.07	T	0.60±0.47	**0.53**	Increaser	TTI
Bupleurum semicompositum L.	FG1	T	0.93±0.38	T	0.47±0.26	0.47	Stable	TTS
Calendula aegyptiaca Desf.	FG1	—	—	T	0.20±0.11	**0.20**	Colonizer	TC
Carduus chevallieri Barratte ex Chevall.	FG1	—	—	T	0.27±0.15	**0.27**	Colonizer	TC
Catapodium loliaceum (Huds.) Link	FG3	T	0.07±0.07	—	—	**0.07**	Loss	TL
Centaurea acaulis L.	FG2	—	—	T	1.00±0.7	**1.00**	Colonizer	TC
Centaurea incana Desf.	FG2	—	—	T	0.27±0.21	**0.27**	Colonizer	TC
Centaurea omphalotricha Coss. & Durieu ex Batt.et Trab.	FG1	—	—	T	0.13±0.13	**0.13**	Colonizer	TC
Centaurea tenuifolia Schleich. ex Steud.	FG2	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Chrysanthemum coronarium L.	FG1	—	—	T	0.87±0.56	**0.87**	Colonizer	TC
Cutandia dichotoma (Forssk.) Trab.	FG3	T	0.67±0.41	—	—	**0.67**	Loss	TL
Dactylis glomerata L.	FG4	—	—	T	1.80±1.31	**1.80**	Colonizer	TC
Ebenus pinnata Aiton	FG1	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Echinaria capitata (L.) Desf.	FG3	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Echium pycnanthum Pomel	FG1	T	0.60±0.41	T	1.00±0.29	**0.40**	Stable	TTS
Eremopyrum cristatum Willk. & Lange	FG4	T	0.27±0.27	T	0.80±0.80	**0.53**	Increaser	TTI
Erodium glaucophyllum (L.) L'Hér.	FG2	—	—	T	1.13±0.94	**1.13**	Colonizer	TC

Erodium triangulare Muschl.	FG1	T	0.27±0.21	T	3.40±1.41	**3.13**	Increaser	TTI
Eruca vesicaria (L.) Cav.	FG1	T	0.47±0.40	T	7.93±2.41	**7.47**	Increaser	TTI
Euphorbia falcata L.	FG1	T	0.20±0.14	T	1.87±0.67	**1.67**	Increaser	TTI
Evax pygmaea Brot.	FG2	T	1.60±0.85	—	—	**1.60**	Loss	TL
Filago germanica L.	FG1	—	—	T	0.33±0.27	**0.33**	Colonizer	TC
Filago spathulata C.Presl	FG1	S	14.13±2.86	S	14.07±4.84	0.07	Stable	SSS
Fumana ericoides Pau	FG2	T	0.13±0.09	—	—	**0.13**	Loss	TL
Genista microcephala Coss. & Durieu	FG5	—	—	T	0.20±0.20	**0.20**	Colonizer	TC
Hedypnois rhagadioloides (L.) F.W. Schmidt	FG1	T	0.20±0.11	T	1.07±0.45	**0.87**	Increaser	TTI
Helianthemum lippii (L.) Dum. Cours.	FG5	T	0.87±0.49	T	0.07±0.07	**0.80**	Decreaser	TTD
Helianthemum salicifolium (L.) Mill.	FG1	T	3.93±1.49	S	18.93±4.75	**15.00**	Increaser	TSI
Herniaria fruticosa L.	FG2	T	0.80±0.54	T	6.13±2.66	**5.33**	Increaser	TTI
Hippocrepis multisiliquosa L.	FG1	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Iris sisyrinchium L.	FG6	T	0.33±0.16	T	1.33±0.42	**1.00**	Increaser	TTI
Juniperus phoenicea L.	FG5	T	1.07±1.07	—	—	**1.07**	Loss	TL
Koeleria pubescens P.Beauv.	FG4	S	24.80±10.47	T	2.53±1.14	**22.27**	Decreaser	STD
Koelpinia linearis Pall.	FG3	T	0.60±0.21	T	0.60±0.35	0	Stable	TTS
Launaea arborescens Murb.	FG5	—	—	T	0.53±0.32	**0.53**	Colonizer	TC
Launaea resedifolia Druce	FG1	T	0.07±0.07	T	1.53±0.45	**1.47**	Increaser	TTI
Lithospermum apulum Vahl	FG1	—	—	T	0.93±0.37	**0.93**	Colonizer	TC
Lolium rigidum Gaudin	FG3	—	—	T	0.33±0.27	**0.33**	Colonizer	TC
Lygeum spartum L.	FG6	T	0.07±0.07	—	—	**0.07**	Loss	TL
Malva aegyptiaca Steud.	FG1	S	35.13±4.61	S	38.80±4.91	3.67	Stable	SSS
Matthiola maroccana Coss.	FG2	T	0.13±0.13	T	0.07±0.07	**0.07**	Decreaser	TTD
Medicago hispida Gaertn.	FG1	T	1.73±1.16	T	1.40±0.45	**0.33**	Decreaser	TTD
Medicago laciniata Mill.	FG1	—	—	T	0.33±0.21	**0.33**	Colonizer	TC
Medicago minima (L.) L.	FG1	—	—	T	0.20±0.20	**0.20**	Colonizer	TC
Micropus bombycinus Lag.	FG1	S	11.20±7.27	T	8.80±3.35	**2.40**	Decreaser	STD
Minuartia campestris L.	FG1	T	0.27±0.18	T	0.47±0.29	0.20	Stable	TTS
Noaea mucronata Asch. & Schweinf.	FG5	S	8.33±3.86	T	2.33±0.95	**6.00**	Decreaser	STD
Papaver hybridum L.	FG1	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Paronychia capitata Lam.	FG2	T	0.40±0.13	T	0.20±0.11	**0.20**	Stable	TTS
Peganum harmala L.	FG2	—	—	T	0.40±0.29	**0.40**	Colonizer	TC
Pituranthos scoparius (Coss. & Durieu) Schinz	FG2	T	1.47±1.47	T	1.47±1.00	0	Stable	TTS
Plantago albicans L.	FG2	S	27.67±11.78	S	15.60±3.17	**12.07**	Decreaser	SSD
Plantago ovata Forssk.	FG1	T	0.53±0.47	T	7.93±3.80	**7.40**	Increaser	TTI
Plantago psyllium L.	FG1	T	0.67±0.54	T	1.40±0.67	0.73	Stable	TTS
Poa bulbosa L.	FG4	T	0.13±0.13	T	0.47±0.27	**0.33**	Increaser	TTI
Pseuderucaria teretifolia O.E.Schulz	FG1	—	—	T	1.93±1.54	**1.93**	Colonizer	TC
Reichardia tingitana (L.) Roth	FG1	T	0.40±0.34	T	0.60±0.29	**0.20**	Stable	TTS
Reseda alba L.	FG1	—	—	T	0.40±0.27	**0.40**	Colonizer	TC
Reseda luteola L.	FG1	—	—	T	0.13±0.13	**0.13**	Colonizer	TC
Rochelia disperma Hochr.	FG1	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Salsola vermiculata L.	FG5	T	0.07±0.07	T	0.80±0.55	**0.73**	Increaser	TTI
Salvia verbenaca L.	FG2	—	—	T	0.93±0.64	**0.93**	Colonizer	TC
Scabiosa arenaria Forssk.	FG1	T	0.60±0.21	T	1.73±1.14	**1.13**	Increaser	TTI
Scabiosa maritima L.	FG1	—	—	T	0.07±0.07	**0.07**	Colonizer	TC
Scabiosa stellata L.	FG3	T	0.07±0.07	T	1.73±1.14	**1.67**	Increaser	TTI
Schismus barbatus (L.) Thell.	FG3	T	6.40±1.53	T	2.40±0.84	**4.00**	Decreaser	TTD
Scorzonera undulata Vahl	FG1	—	—	T	3.00±0.92	**3.00**	Colonizer	TC
Sedum sediforme (Jacq.) Pau	FG2	T	0.20±0.14	T	0.20±0.11	0	Stable	TTS
Sideritis montana L.	FG1	—	—	T	0.67±0.36	**0.67**	Colonizer	TC
Silene rubella L.	FG1	—	—	T	1.40±0.77	**1.40**	Colonizer	TC
Silene tridentata Desf.	FG1	T	0.20±0.14	T	1.13±0.68	**0.93**	Increaser	TTI
Spergularia diandra (Guss.) Boiss.	FG1	—	—	T	0.13±0.13	**0.13**	Colonizer	TC
Stipa lagascae Roem. & Schult.	FG4	S	12.80±8.98	T	5.87±2.32	**6.93**	Decreaser	STD
Stipa tenacissima L.	FG4	D	154.40±18.10	D	165.8±16.89	11.40	Stable	DDS
Stipa tortilis Desf.	FG3	S	15.00±4.87	S	61.00±22.12	**46.00**	Increaser	SSI
Teucrium polium L.	FG2	T	0.07±0.07	T	0.20±020	**0.13**	Increaser	TTI
Thymelaea hirsuta Endl.	FG5	—	—	T	0.80±0.80	**0.80**	Colonizer	TC
Thymelaea microphylla Coss. & Durieu	FG5	T	2.27±1.81	T	0.40±0.40	**1.87**	Decreaser	TTD
Vella annua L.	FG1	T	0.20±0.14	T	4.67±2.42	**4.47**	Increaser	TTI