Biogeosciences
Discussions

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Interactive comment on "Testing functional trait-based mechanisms underpinning plant responses to grazing and linkages to ecosystem functioning in grasslands" *by* S. X. Zheng et al.

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Point-to-Point Response

Reply to Reviewer #3

1. General comments This paper by Zheng and collaborators explores the variation in 9 plant functional traits in grazed and ungrazed grassland communities along a soil resource gradient. They show that trait response to grazing depends on resource availability, and that different life forms show different types of responses to grazing along the gradient. Although not entirely novel, this type of study investigating the interacting effects of resource and grazing on community assembly, functional structure and

ecosystem functioning is still highly relevant. Their approach using response ratios to grazing along the resource gradient seems like a promising way to capture interacting effects. Another asset of this study is the extensive sampling design which accounts for intraspecific trait variations between communities. Moreover, results concerning the different responses of different life-form offer a fresh insight into plant responses to grazing.

Nevertheless, despite these promising ideas, I found the manuscript and results to be confused by a lack of clear justification of hypotheses and interpretation and an unsatisfactory statistical approach. Moreover, after reading the previous paper in Biogeoscience by Zheng et al (2010), I had a hard time seeing a clear distinction and progression in the results. I believe the authors might want to consider refocusing the paper on a few less redundant points. Below are listed the main issues I have with this paper, followed by some specific comments.

Main issues: Unclear use of concepts and lack of justification of interpretations. Expressions such as "mechanisms", "biotic factors", "avoidance and tolerance strategies" are used somewhat lightly and would require better justification and definition in the introduction, but also in the discussion. See detailed comments below.

Reply: We appreciate the reviewer for insightful comments and suggestions on our manuscript. We have revised the Title, Introduction, Results and Discussion sections as suggested by the reviewer. The expressions such as "mechanisms" and "biotic factors" were removed and the "avoidance and tolerance strategies" were clearly defined in the Introduction section.

2. Comments: Page 5 The sources of trait responses/variations (e.g. as on fig 2) are never explained or discussed clearly. Trait variation between communities may arise from 1) species replacement; 2) intraspecific trait variability which may be due to a) plastic responses to grazing and resources, or b) selection of different individual or even ecotypes with genetic differentiation. Differentiation between sources 1) and 2) is

essential for interpretation, and the authors have the necessary data to address it.

Reply: Great point! In the revised manuscript, we analyzed the dissimilarity in species composition (a measure of β-diversity) between the paired ungrazed and grazed communities to examine the effects of species replacement on trait responses. However, the genetic differentiations among different individuals or even ecotypes are beyond the scope of this study. Our results suggest that functional trait variation between communities was mainly arisen from trait plastic responses to grazing and moisture, but not due to species replacement. This is supported by the result that the species dissimilarity showed no consistent trend along the soil moisture gradient (Fig. A2 in the Appendix C). The relevant results and discussions have been added in the revised manuscript.

3. Comments: Statistical analyses are sometimes inappropriate for the data and should be improved. In particular GLM's such as the ones on Table A2 and illustrated in Fig 2 assume independence of data points, whereas data points here are non-independent in two ways: 1) different points belong to the same species 2) measurements along the gradient are grouped per community plot. Therefore, I would recommend performing a mixed model including 2 random factors: species identity and community block. Moreover, it is incorrect to perform repeated individual t-tests (or even ANOVAs) on percentage data such as in fig 5. A global chi-square test would be more appropriate.

Reply: We totally agree with the reviewer that statistical analyses were inappropriate for the data. Thus, we re-analyzed the data using a generalized linear mixed model (GLMM) including two random factors (species identity and communities) and revised Table 2 and Fig. 2 accordingly. To improve the generalization of the results, we used the soil moisture gradient as a continuous variable instead of discussing communities individually. The differences in relative abundance of life forms between the grazed and ungrazed communities varied along the soil moisture gradient were presented in Figure 5. We also revised the Results and Discussion sections accordingly.

4. Comments: The authors should use the continuous environmental gradient in all

analyses, instead of discussing communities individually, or referring to the "three community types". These types are only vaguely defined, and in any case there is not enough repetition per community type to allow any kind of generalization. The continuous gradient, on the other hand, is a good tool when sample size is low, and may provide finer and more generalizable insights.

Reply: Great point. We used the moisture gradient as a continuous variable instead of field holding capacity as per suggested by the reviewer. The results of Figs. 2, 3, 4 and 5 were re-analyzed and presented along the moisture gradient.

5. Comments: Specific comments title: too long and imprecise, please reformulate. I fail to understand what the authors refer to as "trait-based mechanisms"? Mechanisms refer to the causal physiological and developmental response of individuals to their environment and interactions with other individuals, and the consequences in terms of population and community dynamics, none of which are addressed in this study. The trait pattern observed here only hint at possible underlying mechanisms. Moreover, the consequences on ecosystem functioning are also only indirectly assessed here (via proxies such as CWMs).

Reply: We agree with the reviewers that the "mechanisms" and "ecosystem functioning" are not directly and clearly addressed in current study. We have reformulated the title as "Functional trait responses to grazing are mediated by soil moisture, plant functional group identity and composition" in the revised manuscript.

6. Introduction: Page 3 First paragraph: the list of trait interpretations here is not relevant for this first paragraph of introduction, and should be moved to methods. In fact, it would be better to start by defining the different plant strategies of resistance to grazing (tolerant vs. avoidant) very clearly early on, to then be able to introduce the expected association with traits.

Reply: We agree with the reviewer and defined the "avoidance and tolerance strategies" and introduced their expected association with traits in the first paragraph of the

introduction.

7. Page 4 Line 13 :"but also by the biotic factors (e.g., plant species or functional group identity)" I think this use of the term "biotic factors" is misleading. Biotic factors tend to refer more to external biotic interactions with either other plants, or other trophic levels, as opposed to abiotic factors. The "biotic factors" described here refer more to some "internal" factors, which are in fact simply the functional attributes of the species whose response to grazing one is considering. I would advise to remove the expression "biotic factor" altogether from the manuscript, and to refer to the importance of "the identity and functional attributes" of species to predict their response to grazing.

Reply: We appreciate the excellent suggestions made by the reviewer. We removed the term "biotic factor" and emphasized the importance of "plant functional group identity and composition" in the revised manuscript.

8 Comments: Page 5 Lines 16-19: the third question is not really addressed in this study. Mechanisms cannot be inferred directly from the trait patterns.

Reply: We agree with the reviewer and revised the third question as "Third, what are the adaptive strategies of different life forms to grazing and linkage to shifts in functional group composition and community-weighted attributes?".

9. Comments: Methods Page 8 Line 1 "including 106 different species: : :" : I do not understand what "different species" means here. Different from what? The ungrazed sites? Moreover, what is the turnover of species between grazed/ungrazed sites, and also along the gradient? This is essential to interpret the trends in traits along the gradient.

Reply: We agree with the reviewer that description of "106 different species" was not clear. We have revised these sentences as suggested by the reviewer.

"In this study, a total number of 276 species were sampled across six paired plant communities, with 149 species in the ungrazed sites and 127 species in the grazed

sites. There were 113 shared species in both ungrazed and grazed sites.

10. Comments: Line 12-19: "all leaves of an individual: : :" : were leaf traits measured on all leaves, young and old, or only on a selected subset of fully expanded mature leaves (cf. Cornelissen et al 2003; Pérez-Harguindeguy et al., 2013)? What method was used to measure Leaf density?

Reply: In this study, all leaves of an individual were picked and the number of leaves was recorded for measuring leaf density. Then 3–5 fully expanded mature leaves from the same individual were selected for leaf N content and SLA measurements. We have revised the Methods section for clarity in the revised manuscript.

11. Comments: Lines 26-27: I am not sure I understand the justifications for the palatability score. Why not use only the plant palatability index? It seems like the browsing score is more dependent on land-use management practices (number of browsing seasons) and less on inherent properties of the plants?

Reply: We agree with the reviewer that the browsing score is more dependent on land-use practices and less on plant properties. Thus, we only used the plant palatability index and revised Results and Discussion sections accordingly.

12. Comments: Page9 Line 15: Data points are not independent here, and a mixed model (GLMM) would be necessary, with species and communities added as random factors. Moreover, if we cannot disentangle species turnover from intraspecific trait variation then I fail to see the ecological meaning of the trends detected by these models.

Reply: We agree with the reviewer. A mixed model (GLMM) including two random factors (species and community) was performed in the revised manuscript, and the relevant results were also revised. We also analyzed the dissimilarity in species composition (a measure of β-diversity) between the paired ungrazed and grazed communities to examine the effect of species replacement on trait responses to grazing. Our results

showed that functional trait variation between communities is mainly arisen from plastic responses of traits to grazing and moisture, but not due to species replacement. This is supported by the result that the species dissimilarity showed no consistent trend along the soil moisture gradient (Fig. A2 in the Appendix C). We have revised the text in the revised manuscript.

13. Comments: Results Page 10 Line 4: Has any transformation of the data been carried out prior to the PCA ? Fig 1: Why not represent PC2 ? It seems like an important axis, at least as important as PC3, capturing two important traits (SLA and plant Height).

Reply: Data were log10 transformed prior to PCA analysis. We agree with the reviewer that PC2 is an important axis to capture key functional traits, which explained 62.5% of total variance. Hence, we have added PC2 axis in the revised Fig 1.

14. Comments: Line 13-17 : I disagree, PC3 does not capture the leaf economic spectrum (LES). Along the LES, Amax correlates positively with LNC(mass) and SLA, but these tend to be negatively or inversely correlated with Leaf Density (see for example Niinemets 1999). So the positive association of LD and LNC along PC3 are actually in contradiction with the LES.

Reply: We agree that it is inappropriate to define PC3 axis as leaf economic spectrum (LES) in this study. The original sentence has been revised as: "The third principal component (PC3), which explained an additional 14% of the variance, was primarily driven by leaf N content and leaf density, representing an axis of leaf nutrient acquisition and shoot growth".

15. Comments: Lines 23-24: "slightly decreased: : :": this is misleading as the difference is in fact not at all significant (P=0.1)

Reply: We agree the reviewer. The original sentences have been replaced with "Grazing significantly decreased the loading score of plant size along PC1 axis (P = 0.0163),

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but greatly increased PC3 score of leaf N content and leaf density (P = 0.0016). However, the PC2 score of plant height and SLR was little affected by grazing (P = 0.1011)".

16. Comments: Page 11 Lines 6-11: Results from the model, and especially results showing the significant interaction term between grazing and the resource gradient, should not be put into the appendix (table A2) but shown in the main text. These are in my opinion the most interesting results, provided they are maintained when the accounting for random effect of species and plot (see previous comments).

Reply: We agree and removed Table A2 into the main text (as Table 2) in the revised manuscript. A mixed model (GLMM) including two random factors (species and community) was performed to analyze the effects of grazing (G), soil moisture (M), and their interactions on plant functional traits.

17. Comments: Line 26-27: This is strange, palatability usually increases in grassland species with higher leaf nitrogen content and SLA. Moreover, I do not think the palatability score should be used as a functional trait to compare species since it integrates the Browsing season index which refers to external land-use factors, and not the plant functioning itself. This needs to be clarified. Why not use the plants' Palatability Index on its own?

Reply: We agree with the reviewer that palatability score should not be used as a functional trait to compare species since it integrates the browsing season index which refers to external land-use factors, and not the plant functioning itself. Actually, plant palatability is a multidimensional trait, which depends on physical (e.g., toughness, hairiness, thorns and spines) and chemical (e.g., nutritive value, odor, taste and toxins) attributes (Milchunas and Noy-Meir, 2002; Elger and Willby, 2003) and reflects the evolution of plant defense to grazing. Therefore, plant species with higher leaf nitrogen content and SLA may not absolutely have higher palatability.

As suggested by the reviewer, we only used the plant palatability index in the revised manuscript and revised the results and discussion sections accordingly.

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18. Comments: Page 12 Lines 11-12 :" The effects of grazing on plant functional group composition differed across different vegetation types" : no proper statistical test. Figure 5 indicates that differences between grazed and ungrazed were tested by "ANOVA"? Where are the anova results shown? Do the stars represent multiple post-hoc t-tests? These tests are performed on percentage data, and an overall chisquare test performed for each community type would be more appropriate to test changes in life form proportions with grazing.

Reply: We appreciate these suggestions made by the reviewer. In order to improve the generalization of the results, we use the soil moisture gradient as a continuous variable instead of discussing communities individually. The results showed that the differences in relative abundance of life forms between the grazed and ungrazed communities varied significantly along the soil moisture gradient (see Figure 4 for detail).

19. Comments: Lines 23-24: How were these comparison tested? Since there is no real replications for each community type (the quadrats constitute only pseudo repli-cates), the t-tests do not seem like the most appropriate method. It would be more interesting to look at how these CWM vary along the gradient, or rather how the differ-ence in CWM between grazed and ungrazed vary along the gradient.

Reply: We agree with the reviewer that it seems the most appropriate to look at how these CWM vary along the soil moisture gradient. To improve the generaliza-tion of the results, we used the soil moisture gradient as a continuous variable in-stead of discussing communities individually. The results showed that the differences in community-weighted attributes between grazed and ungrazed communities varied significantly along the soil moisture gradient (see Figure 5 for detail).

20. Comments: Discussion Page 13 Line 9: these PCA axes, though interesting, may not be interpreted as "spectrums" in the same way the leaf economic spectrum is discussed. The LES has been defined over multiple studies, and on a much broader dataset. It also refers to a clearly identified evolutionary trade-off. Please reformulate.

Reply: We agree that the "spectrums" is generally based on a broader dataset over multiple studies, which is not rigorously used in this study. We have deleted the ex-pression of "spectrums", and rephrased the relevant sentences.

21. Comments: Page 14 Lines 6-7: ": : : indicating that plant species exhibit both avoidance and tolerance strategies to grazing" I fail to see how a decrease in height and increase SLA necessarily indicate a mixed avoidance and tolerance strategy, or even any kind of strategy in response to grazing at all. Interpreting all trait patterns in terms of strategies ignores the fact that trait variations may be non-adaptive or plastic.

Reply: We appreciate this point by the reviewer.

Previous studies propose that plant species may adopt some avoidance (escape from grazers) and tolerance (regrowth capacity after defoliation) strategies to improve their grazing resistance (Strauss and Agrawal, 1999; Díaz et al., 2001; Cingolani et al., 2005; Díaz et al., 2007). Plant height, individual biomass, and stem-leaf biomass ratio are associated with biomass allocation and species' capacity for light competition (Poorter and Nagel, 2000; Cornelissen et al., 2003), and also linked to plant avoidance strategies to grazing (Díaz et al., 2001; Adler et al., 2004). Grazing avoidance traits are usually related to small plant size, such as small height and low individual biomass to decrease feeding selectivity of herbivores (Díaz et al., 2001; Cingolani et al., 2005). Leaf N content and specific leaf area (SLA) are tightly linked to leaf nutrient acquisition and turnover and potential growth rate (Reich et al., 1999; Wright et al., 2004), as well as plant tolerance strategies to grazing (Díaz et al., 2001; Zheng et al., 2011). Grazing tolerant traits are usually associated with high leaf N content and SLA to increase shoot regrowth capacity (Strauss and Agrawal, 1999; Pérez-Harguindeguy et al., 2003)."

In this study, for most species, plant height was decreased, but leaf N content and SLA were increased by grazing across six communities along the soil moisture gradi-ent. This indicates that plant species exhibit both avoidance and tolerance strategies to grazing (Díaz et al., 2001; Adler et al., 2004; Zheng et al., 2011). In a previous

study, we examined plant functional traits of two dominant species, Leymus chinensis (C3 perennial rhizome grass) and Cleistogenes squarrosa (C4 perennial bunchgrass), based on a long-term grazing experiment (Zheng et al., 2011). Our results showed that plant height and leaf size of both species decreased with increasing stocking rate, which reduced foraging selectivity by herbivores (Vesk et al. 2004). While the SLA, leaf Nmass and Narea of both species increased or relatively unchanged under high grazing pressure, which might be favorable for leaf turnover and shoot regrowth (Cingolani et al. 2005; Evju et al. 2009; Pérez-Harguindeguy et al. 2003; Westoby 1999). These results also suggest that plant species exhibit both avoidance and tolerance strategies to grazing.

Hence, plant functional traits can provide important insights into the adaptive strategies of plant species to grazing, which has been corroborated by several previous studies. We also agree that plant strategies to grazing are just indirectly reflected by functional traits in these studies, and the non-adaptive or plastic variations in plant traits were generally not considered.

22. Comments: Page 15 Whole paragraph 4.3: These interpretations of plant response are speculative and do not constitute mechanisms as no measure of tolerance or avoidance is really measured. Please reformulate.

Reply: We agree with the reviewer and revised these sentences as suggested in the revised manuscript.

23. Comments: Line 26 " the annuals and biennials with high growth rate adopted more tolerant strategies: : :". Please reformulate this sentence. Plants species do not "adopt" strategies willingly.

Reply: The sentence has been revised as "the annuals and biennials with high growth rate exhibited more tolerant strategies. . . . . .".

24. Comments: Line 9-11: I do not understand this sentence. "Second, the peren-

nial grasses exhibited greater grazing tolerance but due to rapid regrowth capacity, indicated by the increased SLR, SLA and leaf N content, and high palatability scores."

Reply: We have revised this sentence for clarity.

25. Comments: Page 16 Line 6-7: the concept of mixed strategies should be clearly defined earlier in the introduction, along with expected trait patterns.

Reply: We appreciate this point by the reviewer. We have provided more detailed interpretation on the mixed strategies in the Introduction section.

26. Comments: Line 9: "It is known that SLA is a relatively stable functional trait,: : :" Stable in what way? It has rather been shown to vary with environmental conditions, and it is evolutionary quite labile (Flores et al. 2014). Please justify this sentence.

Reply: We agree that the sentence is misleading, and we have rephrased the sentence (as following) and moved it to the Introduction section.

It is widely recognized that high SLA is associated with high potential growth rate (Reich et al., 1999; Wright et al., 2004), resource acquisitive strategies (Díaz et al., 2004; Tecco et al., 2010), and plant tolerance to grazing (Díaz et al., 2001; Zheng et al., 2011). Low SLA, in contrast, is tightly related to physical toughness (Villar and Merino, 2001; Wright et al., 2004), resource conservative strategies (Díaz et al., 2004; Tecco et al., 2010), and plant resistance to grazing (Hanley et al., 2007).

27. Comments: Line 13: LMA is the same trait as SLA (the inverse), there is no need to mention both.

Reply: Revised accordingly.

28. Comments: Page 17 Lines 2-3 : "Our findings indicate that the grazing-induced shifts in functional group composition are largely dependent on site productivity, particularly water availability": This result is not shown in the manuscript. Responses in life form proportions would need to be tested along the soil gradient. Lines 13-15: what

are the consequences of these trends in CWM ? How do the authors interpret them apart from changes in growth forms?

Reply: As suggested by the second reviewer, we conducted a CCA analysis to quantify to what extent soil moisture influences plant community structure on the basis of relative abundance of different life forms. Our findings indicate that the grazing-induced shifts in functional group composition are largely dependent on site productivity, particularly water availability. The soil moisture explained 90% of total variance in plant community structure.

29. Comments: Page 18 Line 9-10: "the increase in prolonged droughts together with heavy grazing may accelerate the shifts in dominance from perennial rhizomatous grasses to perennial bunchgrasses in the typical steppe and consequently decrease biodiversity and ecosystem functioning and services." Why would this shift in composition decrease biodiversity and ecosystem services?

Reply: The perennial rhizomatous grasses (e.g., Leymus chinensis) and perennial bunchgrasses (e.g., Stipa grandis, Agropyron cristatum, Cleistogenes squarrosa,) are the dominant life forms in the Inner Mongolia grasslands. The perennial bunchgrasses, mostly xerophytes, are more resistant to grazing than perennial rhizomatous grasses (mostly mesoxerophyte) in terms of avoidance and tolerance traits, particularly under heavy grazing pressure and in dry years (Zheng et al. 2011). Moreover, the perennial bunchgrasses exhibit more conservative resource-use strategies (low leaf N content and SLA) in dry and infertile habitats. Previous studies in the same area demonstrated that heavy grazing shifted plant species and functional group composition, reduced plant species richness, primary production, soil coverage, and increased vulnerability to soil and water erosions (Wan et al. 2011; Schönbach et al. 2011; Kölbl et al. 2011). Hence, the increase in prolonged droughts together with heavy grazing may accelerate the shifts in dominance from perennial rhizomatous grasses to perennial bunchgrasses in the typical steppe. We have added the above mentioned information in the revised manuscript.

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Kölbl, A., Steffens, M., Wiesmeier, M., Hoffmann, C., Funk, R., Krümmelbein, J., Reszkowska, A., Zhao, Y., Peth, S., Horn, R., Giese, M., and Kögel-Knabner, I.: Grazing changes topography-controlled topsoil properties and their interaction on different spatial scales in a semi-arid grassland of Inner Mongolia, P.R. China, Plant Soil, 340, 35-58, doi: 10.1007/s11104-010-0473-4, 2011.

Schönbach, P., Wan, H. W., Gierus, M., Bai, Y. F., Müller, K., Lin, L. J., Susenbeth, A., and Taube, F.: Grassland responses to grazing: effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem, Plant Soil, 340, 103-115, doi: 10.1007/s11104-010-0366-6, 2011.

Wan, H. W., Bai, Y. F., Schönbach, P., Gierus, M., and Taube, F.: Effects of grazing management system on plant community structure and functioning in a semiarid steppe: scaling from species to community, Plant Soil, 340, 215-226, doi: 10.1007/s11104-010-0661-2, 2011.

Zheng, S. X., Lan, Z. C., Li, W. H., Shao, R. X., Shan, Y. M., Wan, H. W., Taube, F., and Bai, Y. F.: Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China, Plant Soil, 340, 141-155, doi: 10.1007/s11104-010-0369-3, 2011.

For the detailed changes we have made, please see the supplement files that includes (1) reply to Reviewer #3, (2) revised manuscript, and (3) revised supplementary material.

Please also note the supplement to this comment: http://www.biogeosciences-discuss.net/11/C8607/2015/bgd-11-C8607-2015-supplement.zip

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Interactive comment on Biogeosciences Discuss., 11, 13157, 2014.