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Desertification and nitrogen addition cause species homogenization in a desert steppe ecosystem

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ABSTRACT

Although the influences of desertification and nitrogen (N) addition in shaping species composition and community structure have long been explored, our understanding of the underlying processes is not yet strong. Analyses of trends in the turnover and nestedness components of beta diversity can be informative of the processes response to N addition and desertification in desert steppe ecosystems. Our investigation of the changes in beta diversity under desertification and N addition in a desert steppe ecosystem in northern China showed desertification to significantly decrease beta diversity among communities, which leads to species homogenization. Further, decreases to the turnover component of beta diversity was likely an important factor causing homogenization under desertification. Although nitrogen addition did not fundamentally influence beta diversity, dissimilarity caused by nestedness significantly increased with nitrogen addition. The contrasting effects of desertification and N addition on the turnover and nestedness components of beta diversity suggest that the ordered loss of plant species with desertification improvement. Overall, our findings provide strong evidence that the effects of desertification and N addition on beta diversity change with ecological processes. We recommend that conservation strategies that focus management practices on prevention of desertification will be most effective in maintaining species diversity.

1. Introduction

Desertification is severe land degradation in arid and semi-arid regions (Verón and Paruelo, 2010). One of the its significant consequences is loss of biodiversity in the desert steppe ecosystem (Ulrich et al., 2014; Xu et al., 2015), and this could have far-reaching effects on ecosystem functioning and services (Chen et al., 2016; Gossner et al., 2016). Previous experimental studies have revealed that desertification can decrease plant diversity per site and reduce beta-diversity across sites, reflecting species homogenization (Maestre et al., 2012; Ulrich et al., 2014; Gossner et al., 2016; Tang et al., 2017). This species homogenization might occur through reducing differences between communities (i.e., either loss of rare or specialized species), increasing similarity (i.e., a gain of generalist, widespread species), or most likely a combination of both (McKinney and Lockwood, 1999; Smart et al., 2006; Gámez-Virués et al., 2015; Gossner et al., 2016). N addition is one of major threats to biodiversity and ecosystem services in terrestrial ecosystems, especially within arid and semi-arid regions (Elser et al., 2007; Lan and Bai, 2012), and nitrogen addition likewise decreases species richness and beta-diversity promote species homogenization by favoring the same few species with traits enabling the exploitation of extra nitrogen (Lan and Bai, 2012; Xu et al., 2015). Ecologists generally consider loss of beta diversity to result in loss of rare or specialized species (Myers et al., 2013; Gossner et al., 2016). However, the underlying processes of decreases in beta diversity caused by nitrogen addition and desertification remain to be resolved. Prior studies of beta diversity loss with nitrogen addition and desertification focused on total beta diversity, the total change in species composition between sites, but partitioning of beta diversity into spatial turnover and nestedness could provide insights about how stressed communities change.

The idea that beta diversity may reflect two different ecological phenomena: spatial species turnover and nestedness of assemblages (Harrison et al., 1992; Baselga, 2007) is not new. Baselga (2010) developed methods for additive partitioning analyses of beta diversity

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into spatial turnover and nestedness components, which result from two antithetic processes. Species assemblages are considered nested when the communities within species-poor sites are subsets of the communities within species-rich sites (Wright and Reeves, 1992; Ulrich and Gotelli, 2007). Nestedness, a relative quantification of dissimilarity between plant communities due to the effects of nesting patterns, reflects non-random species loss due to any factor that promotes the orderly disaggregation of community assemblages (Gastón and Blackburn, 2008). Spatial turnover occurs when some species are replaced by others as a consequence of environmental sorting or spatial and/or historical constraints (Qian et al., 2005). Changes in beta-diversity can thus result from two distinct patterns of extinction and invasion.

Intensification of desertification and nitrogen addition may have differential effects on the spatial species turnover and nestedness components of beta diversity. For example, intensified desertification can decrease species diversity and species richness, resulting in changes to community composition, and, therefore, the nestedness component of beta diversity (Lechmere-Oertel et al., 2005; Ibanez et al., 2015). On the other hand, desertification intensification could also increase environmental heterogeneity and decrease resource availability and species. Only a few species which are adapted to poor site conditions can survive and became dominant with desertification intensification, resulting in decreases to the turnover component of beta diversity (Bestelmeyer, 2005, Ulrich et al., 2014). In contrast, as a result of changes to soil resource availability, soil nutrients may affect few species with particular traits that enable them to exploit the additional N, and therefore reduce turnover and/or nestedness. However, spatial species turnover and nestedness may not be affected by N addition when N levels are low (Gossner et al., 2016). Up to now, these concepts have not been well studied. Therefore, examining the effects of desertification intensification and nitrogen addition on different components of beta diversity is critical to identify the multiple underlying processes.

Here we apply Baselga's methods to community change in arid ecosystems in China under stress from desertification and nitrogen addition. Combining observational studies of sites subject to different levels of desertification with experimental addition of nitrogen, we have a factorial system in which the two effects can be separated. Under the hypothesis that nitrogen addition favors a few species able to exploit added N (Gossner et al., 2016), spatial turnover would decline but not nestedness (Bestelmeyer, 2005; Ulrich et al., 2014). The stress of desertification, meantime, is predicted to cause loss of rare species found at a few diverse sites, leading to a reduction in nested beta-diversity (Lechmere-Oertel et al., 2005; Ibanez et al., 2015).

2. Materials and methods

2.1. Study area

The study area is located in Yanchi County (37°–38°N, 106°–107°E, elevation 1450 m). It is a desert steppe in the southwestern of the Mu Us sandy land in China. This region possesses a semi-arid temperate climate which produces a mean annual temperature at 8.1 °C, a mean annual precipitation is 295.1 mm. The soil types of the study site are orthi-sandic entisols, sierozem, and loess. Because all of the soil types are characterized by low fertility and loose structure, so all types of soil are very susceptible to wind erosion. The predominant species in this region are *Agriophyllum squarrosum* (L.) Moq. *Corispermum hyssopifolium* L., *Artemisia scoparia Waldst.* et Kit., *Salsola collina* Pall., *Leymus secalinus* var. *secalinus*., *Pennisetum centrasiaticum* Tzvel., and *Cleistogenes gracilis* Keng..

3. Experimental design

The study design employed space-for-time substitution. Four sampling areas representing four different desertification stages, namely, potential desertification (PD, non-degraded), light desertification (LD, fixed dune), severe desertification (SD, semi-mobile dune), and very severe desertification (VSD, mobile dune), were randomly chosen based on the criteria described by Li et al. (2006). For each stage of desertification three sites with a similar condition were selected. Within each sampling area, four study sites with similar conditions and that exceeded 50 × 50 m dimensions (approximately 0.2 km away from one another) were selected. We randomly established six 4 × 4 m plots at the approximate center of each study site. Three of these plots were fertilized with N and the remaining three plots were controls. N was applied in the form of ammonium nitrate (NO_3NH_4, 10 g·m^{-2}·yr^{-1}) on April 25th. At the center of each plot we established a 1 × 1 m quadrat by fixing one PVC (Polyvinylchloride) pipe in each corner of the plot, for community monitoring. Field surveys were performed monthly from May to August (from the 25th to 30th of each month) in 2015 and 2016. In the 1 × 1 m quadrat that we established at the center of each plot, plant species richness were recorded every month. Using a second nearby quadrat for destructive sampling, the above-ground structures of all green plants were cut, placed into envelopes, tagged, then bring back to the lab. The above-ground structures of green plants were immediately oven-dried for 72 h at 65 °C before being weighed. Total dry biomass of every species was recorded.

4. Statistical analyses

Beta diversity was quantified as the dissimilarities among all control plots and fertilized plots within each site of each single month, using Jaccard's dissimilarity, an incidence-based metric. Within each site, mean dissimilarity between each pair of plots was computed to examine whether beta diversity was influenced by desertification and N addition. Then we partitioned beta diversity into turnover and nestedness components following the methods of Baselga (2010) provided in the R statistical package "betapart" (Baselga et al. 2012). Partiting beta diversity into turnover and nestedness components as follow method:

$$\beta_{jac} = \beta_{jtu} + \beta_{jne}$$

$$\beta_{jtu} = \frac{2b}{2b + a}$$

$$\beta_{jne} = \left(\frac{c - b}{a + b + c}\right)\left(\frac{a}{2b + a}\right)$$

where, β_{jac} is beta diversity; β_{jtu} is turnover; β_{jne} is nestedness components; a is the number of species common to both plots, b is the number of species that occur in the first plot but not in the second and c is the number of species that occur in the second plot but not in the first.

A null-model approach was used to compare the observed values to the expected ones. An independent swap algorithm was used to create a null model (Gotelli, 2000; Ulrich and Gotelli, 2007), and swap algorithm can maintain constant species richness within each community and constant species occurrence among communities while simulating species assemblages in each plot by randomly sampling species from the local species pool (Crist et al., 2003; Kraft et al., 2011; Li et al. 2016). Null modeling was conducted using the "vegan" package in R (Oksanen et al., 2015). For each plot, we obtain a null distribution of beta diversity (as well as the associated nestedness and turnover components) through the procedure was iterated 999 times. We calculated the standardized effect size (beta deviation) divided by the standard deviation of the expected values as the difference between the observed and expected scores of any statistic, (Kraft et al., 2011; Myers et al., 2013; Li et al., 2016). An observed pattern is considered not differ from randomness when a beta deviation of zero, whereas negative and positive beta deviation indicate lower and higher beta diversity than expected by chance, respectively.

We tested for differences in observed beta diversity, observed turnover, observed nestedness, expected beta diversity, expected turnover, expected nestedness, beta deviation, turnover deviation, and nestedness deviation among different desertification stages and between N addition and control plots using multilevel regression modeling under an hierarchical Bayesian framework, with sampling time treated as random error and both nitrogen desertification stages as fixed effects.

The hierarchical (or multilevel) ANOVA as follows:

The *y* (beta diversity) was the response variable, and it was modeled for each desert stage i as

$$y \sim N(\mu_i, \sigma_y^2)$$

that is, a stochastic variable with expected value μ_i and a normally distributed site error term.

$$\mu_i = \beta 0 + \beta 1_{j(i)} * [N]_i + \beta 2_{j(i)} * [Desertification]_i + \beta 3_{j(i)} * [N]_i * [Desertification]_i + \varepsilon_i$$

where $\varepsilon \sim N(0,\sigma^2)$.

We implemented multilevel regression modeling using JAGS and the R2jags package in R v3.0.2 (Su and Yajima, 2015). Four independent Markov chain Monte Carlo (MCMC) simulations of 100 000 steps were run, and the first 10 000 iterations were discarded. Convergence of parameter estimates was confirmed by visually examining the trace plots of the chain iterations and by ensuring the values of the Brooks-Gelman-Rubin statistic were less than 1.1. Further details of the modeling process are described in Appendix A (R code).

5. Results

Desertification significantly decreased the observed beta diversity among plots (Fig. 1A, S2), which suggests that desertification leads to species homogenization. In fact, desertification accounted for 40% of the finite population variance components of observed beta diversity (Fig. 1a). Moreover, although the trends in expected beta diversity were similar to the trends in observed beta diversity (Fig. 2A), desertification accounted for 35% of the finite population variance components of expected beta diversity (Fig. 2a). In contrast, N addition decreased the observed beta diversity among plots. N addition accounted for 9% and 10% of the finite population variance components of observed and expected beta diversity, respectively. However, N addition did not significantly affect beta-diversity (Fig. S2).

When beta diversity was partitioned into spatial turnover and nestedness components, result showed that both observed and expected spatial turnover component significantly decreased with desertification development (Fig. 1B). Desertification accounted for 30% of the finite population variance components of observed spatial turnover component. And the finite population variance components of expected spatial turnover component increased to 38%. However, spatial turnover component did not significantly change with N addition (Fig. S3). In contrast, the observed nestedness increased with intensifying desertification. Desertification accounted for 23% and 43% of the finite population variance components of observed and nestedness components. N addition significantly affect observed nestedness (Fig. S4), which accounted for 25% and 8% of the finite population variance components of observed and nestedness components.

In the non-N addition plots, the beta deviation (Fig. 3A, S8) were negative for all stages of desertification, reflecting more similar species composition. However, in N addition plots, beta deviation was not different from zero for all desert stage except LD stage (Fig. 3A). Further findings were that both nestedness deviation and turnover deviation were significantly different from zero in PD stage (Fig. 3B and C). N addition have big effect on nestedness deviation and turnover deviation. We found both nestedness deviation and turnover deviation were change in opposite directions combined N addition plots with non-N addition plots. The contrasting effects of nitrogen addition and desertification on the nestedness and species turnover components of beta diversity suggest that the decrease in species diversity due to desertification will be mitigated by nitrogen addition.

Both N addition and the interaction between desertification stage and N addition significantly affected nestedness deviation and turnover deviation (Figs. S9, S10). N addition and the interaction between desertification and N addition, respectively explained 40% and 30% of the variance components of the nestedness deviation (Fig. 3c), and 30% and 20% of the variance components in the turnover deviation (Fig. 3b).

6. Discussion

6.1. Effect of desertification on beta diversity, spatial turnover, and nestedness

This investigation of the effects of desertification on beta diversity and its components (turnover and nestedness) showed desertification to exert strong negative effects on beta diversity. These results suggest that species homogeneity, and community structure tend to converge with intensifying desertification. Spatial turnover and nestedness components of beta diversity played important roles in determining community composition across desertification stages. The impact was principally through spatial turnover, indeed the nestedness component of beta diversity increased with desertification. The influence of the two processes underlying measurements of beta diversity (i.e., species loss and replacement) not only differed, but was also antithetic. Those antithetic process showed that the ordered loss of plant species with desertification improvement. This indicates that with intensifying desertification dissimilarity was largely driven by variation in community composition, rather than differences in taxonomic richness i.e. nestedness-resultant (Viana et al., 2016).

The decline in beta diversity with desertification observed in this study is consistent with other results (Gossner et al., 2016). Desertification leads to species homogenization through loss of rare or specialized species, gains in widespread generalist species, and, most likely, a combination of the two (Smart et al., 2006; Karp et al., 2012; Gámez-Virués et al., 2015; Gossner et al., 2016). The four sites investigated here were at different desertification stages and varied in conditions, so therefore favored different subsets of species. This resulted in considerable variation in community structure among sites. A previous study showed that desertification was a major driver of environmental heterogeneity (Tang et al., 2016), and that the deterministic nice-selective forces are important factors influencing beta diversity with across desertification stages.

In this study, we found desertification had a larger effect on spatial turnover than nestedness. This may be due to dispersal limitations and/or deterministic processes, such as environmental or habitat filtering, and supports the theory that declines in spatial turnover are caused by increases in environmental heterogeneity and nice-selective forces, which led to declines in beta diversity (Qian et al., 2005). Because, in desert steppe, with relatively low species richness and density, it may be that only a few species which are adapted to poor site conditions can survive and became dominant with desertification intensification. A second explanation is that stochastic process plays an important role influencing spatial turnover, which is consistent with our null expectation. However, we found intensity of desertification to significantly influence spatial turnover only at initial stages of desertification; further desertification did not increase spatial turnover, supporting the conclusion that minimizing desertification is the most effective strategy to enhance beta diversity. This finding is consist with the findings of Gossner et al. (Gossner et al., 2016), i.e., that variation in land-use intensity influenced turnover only at low land-use intensities; further increases in intensity did not increase beta diversity.

In contrast, we found the nestedness component of beta diversity to

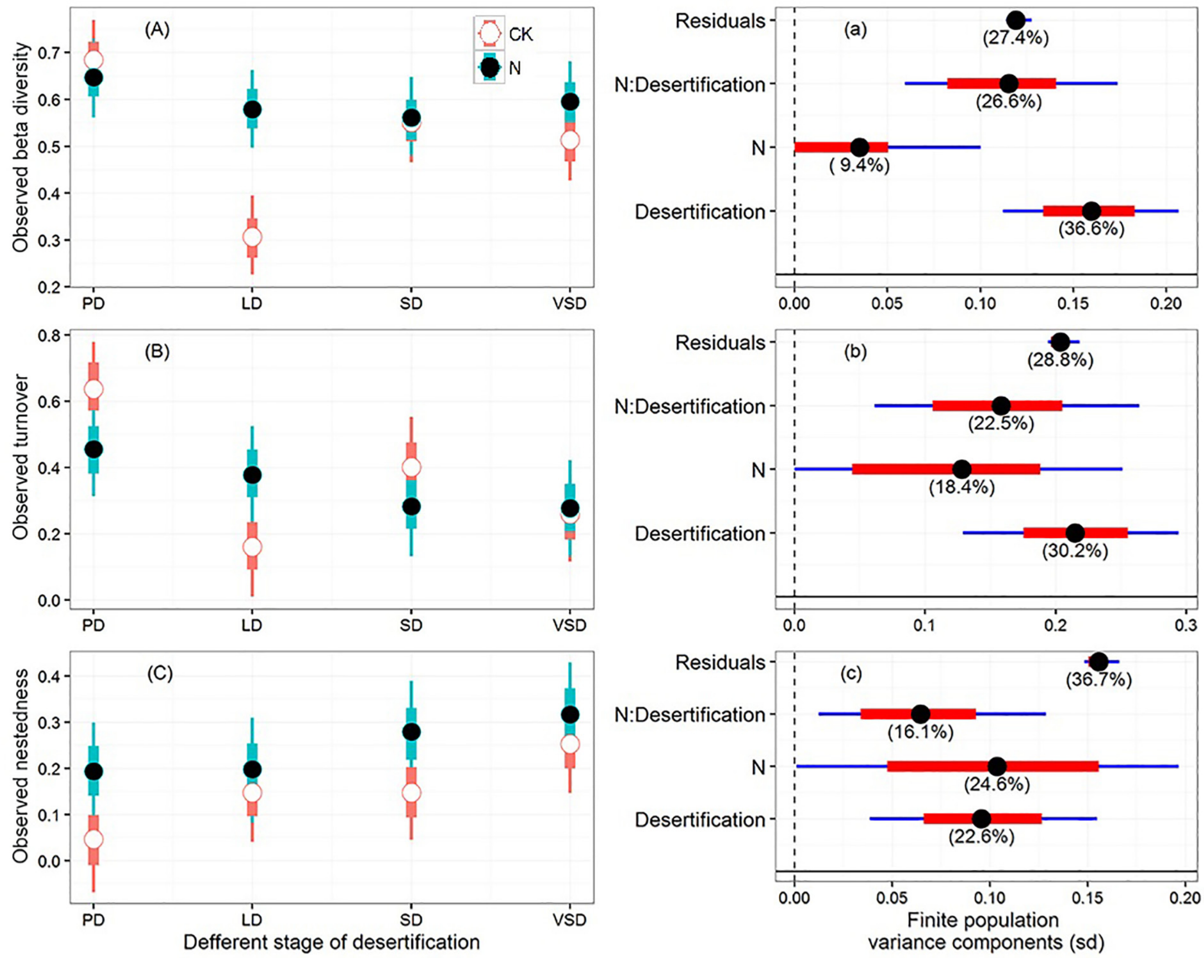

Fig. 1. Observed beta diversity, spatial turnover, and nestedness within different desertification stages and explained by desertification and N addition. A, observed beta diversity; a, finite population variance components of observed beta diversity; B, observed spatial turnover; b, finite population variance components of observed spatial turnover; C, observed nestedness; c, finite population variance components of observed nestedness. Circles denote medians estimated by hierarchical mode, thick lines denote 68% posterior credible intervals, and thin lines denote 95% posterior credible intervals. Abbreviations are: PD, potential desertification; LD, slight desertification; SD, severe desertification; VSD, very severe desertification.

increase with desertification intensification, reflecting growing dissimilarity between nested communities produced by increasing differences in the number of species between sites. Species diversity decreased through a loss of rare or specialized species (Gossner et al., 2016), thereby reducing the possibility of communities sharing the same species and niche overlaps between species. This led to greater difference in the number of species between sites, and increased dissimilarity between nested communities with desertification intensification (Baselga, 2010). An alternative explanation is that stochastic processes influenced the nestedness component of beta diversity (Ulrich and Gotelli, 2007). This pattern is consistent with the null expectation that stochastic processes play important roles influencing local species assemblages, as relatively low degree of species diversity were increase stochastic distribution of plant result in increasing dissimilarity between vegetation communities.

7. Effect of N addition on beta diversity, spatial turnover, and nesteness

N addition has been observed to negatively influence species diversity in a variety of studies (Stevens et al., 2004; Harpole et al., 2007; Eskelinen and Harrison, 2015; Tang et al., 2017). Although we found no significant effect of N addition on spatial turnover or beta diversity, increases in N addition did have positive influences on the nestedness component of beta diversity. Similar declines in species diversity with N addition were observed in this study. These results suggest that N addition promoted disaggregation of the plant communities (Gastón and Blackburn, 2008). Both N addition and the interaction between desertification stage and N addition significantly affected nestedness deviation and turnover deviation. However, we found beta diversity as well as nestedness and spatial turnover components of beta diversity were not associate with the interaction between desertification and N addition. It is possible that no significant change on beta diversity or spatial turnover in the site where N is main limiting factor when N levels are low. However, the interaction between desertification and N addition did significantly affect species composition. We found both nestedness deviation and turnover deviation were change in opposite directions combined N addition plots with non-N addition plots. The contrasting effects of nitrogen addition and desertification on the nestedness and species turnover components of beta diversity suggest that the decrease in species diversity due to desertification will be mitigated by nitrogen addition. The effect of N addition on species composition is likely through modification of the microenvironment in the desert steppe ecosystem where N is a limiting nutrient (Harpole et al., 2007; Zhang et al., 2011; Xu et al., 2015; Tang et al., 2017).

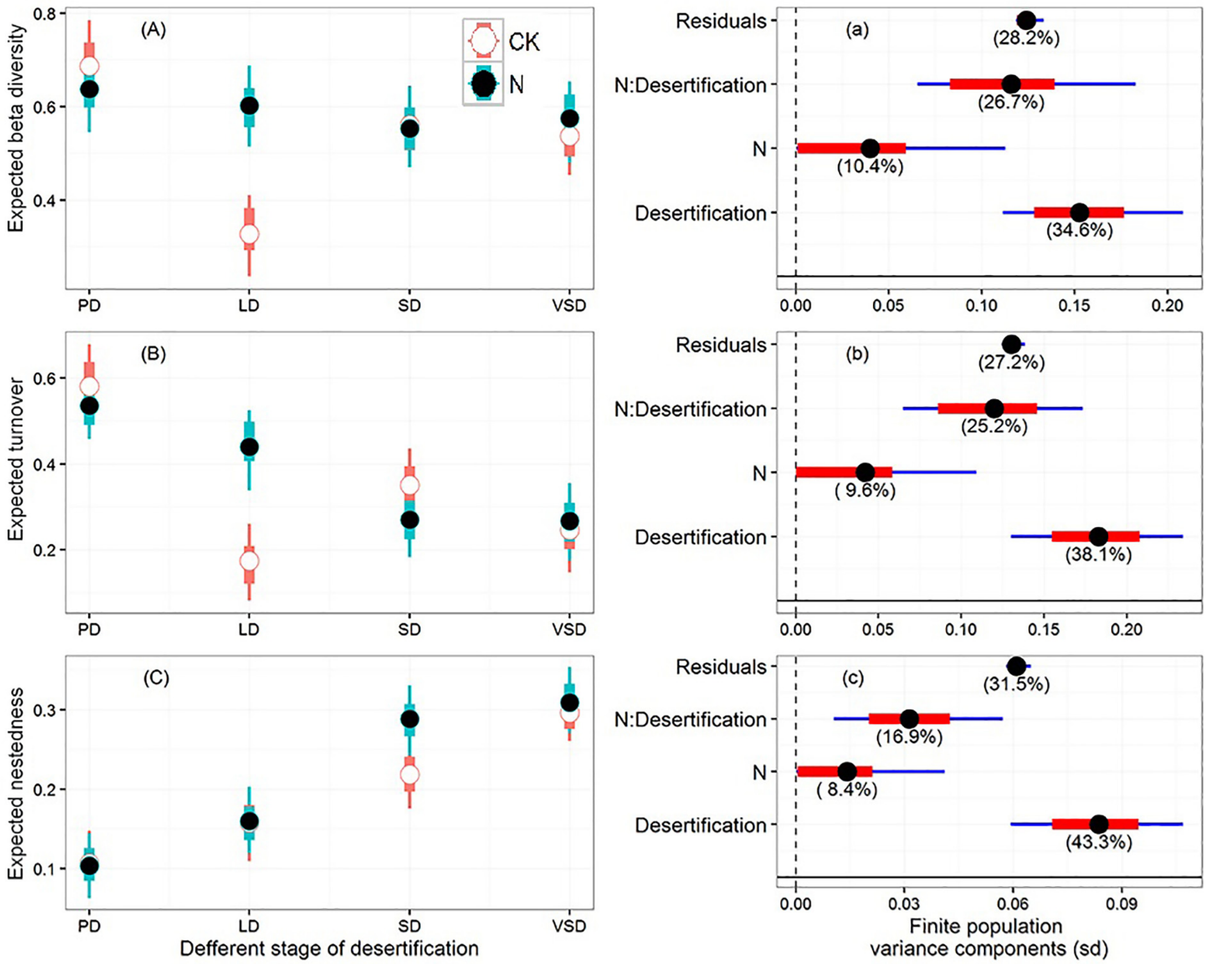

Fig. 2. Expected beta diversity, spatial turnover, and nestedness within different desertification stages and explained by desertification and N addition. A, expected beta diversity; a, finite population variance components of expected beta diversity; B, expected spatial turnover; b, finite population variance components of expected spatial turnover; C, expected nestedness; c, finite population variance components of expected nestedness. Circles denote medians estimated by hierarchical model, thick lines denote 68% posterior credible intervals, and thin lines denote 95% posterior credible intervals. Abbreviations are: PD, potential desertification; LD, slight desertification; SD, severe desertification; VSD, very severe desertification.

8. Caveats to the study

Although the observed patterns in beta diversity and its nestedness and turnover components are accord with our predictions, there are several limitations should be noted to this study. First, this study only attention to chronosequences by employing a space-for-time substitution approach inferring temporal trends from sites at different stages of desertification. Furthermore, one of the treatment used space-for-time approach to study the effect of desertification of species diversity, however, another treatment we used to study the effect of N addition on species diversity, which is not a fair comparison. Future studies integrating long-term monitoring of species composition would provide important information for explaining the processes of desertification. And, in order to reveal the influence of desertification and N addition on species diversity, future studies should study this topic separately. Such studies would provide stronger evidence to gain additional insight into the processes underlying plant community assembly.

9. Conclusions

In conclusion, our findings provide evidence that desertification intensification and N addition affect beta diversity. Desertification significantly decreased beta diversity among communities, which led to species homogenization. Furthermore, a decrease in the turnover component of beta diversity was likely a major factor causing homogenization under desertification. The contrasting effects of nitrogen addition and desertification on the nestedness and species turnover components of beta diversity suggest that the decrease in species diversity due to desertification will be mitigated by nitrogen addition. Therefore, the underlying processes of beta diversity caused by nitrogen addition and desertification provide a unique way to understand the underlying variation of species composition among sites, which may provide important guideline for combating desertification and nitrogen enrichment.

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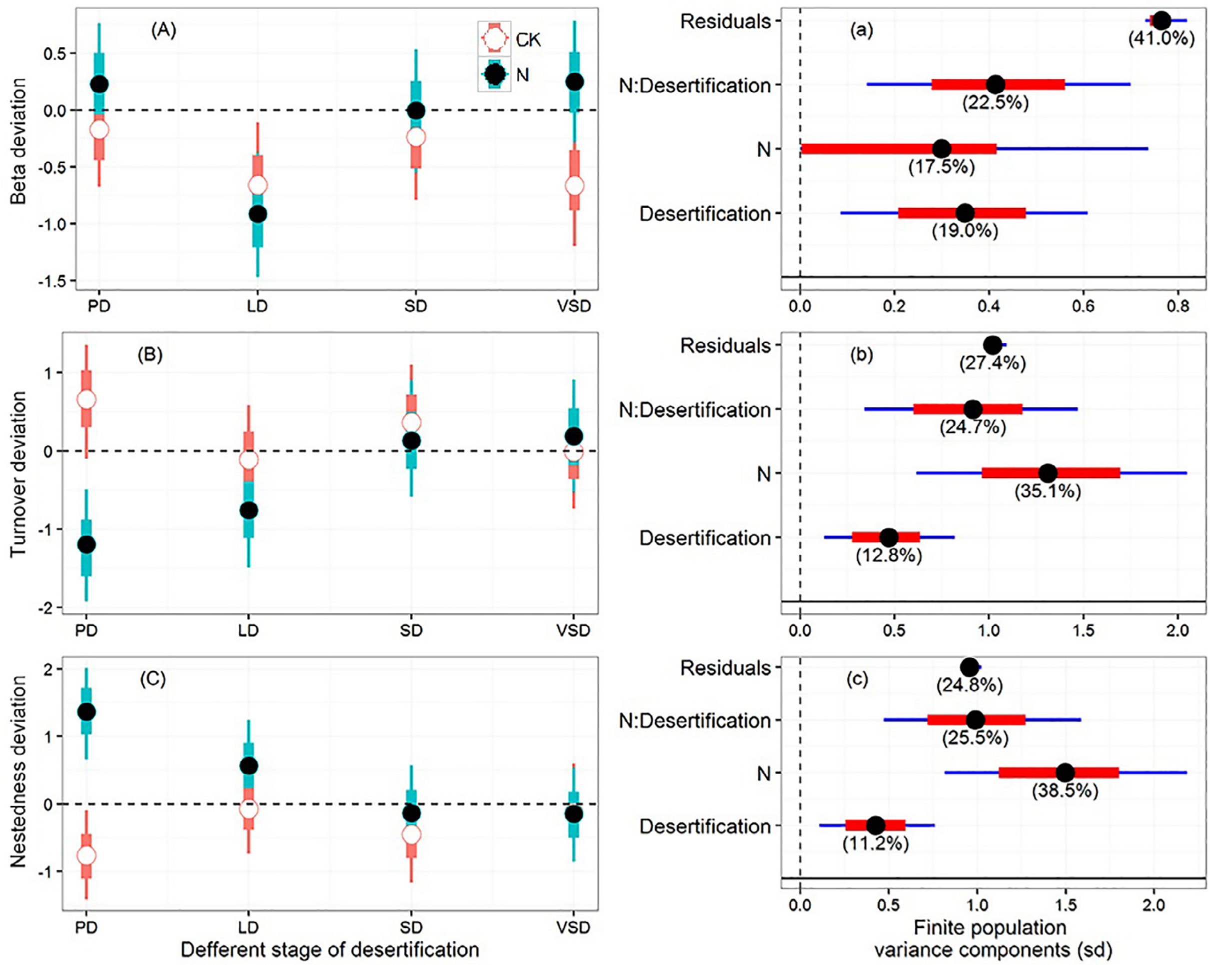

Fig. 3. Beta deviation, spatial turnover deviation, and nestedness deviation in different desertification stage and them explained by desertification and N addition. A, beta deviation; a, finite population variance components of beta deviation; B, spatial turnover deviation; b, finite population variance components of spatial turnover deviation; C, nestedness deviation; c, finite population variance components of nestedness deviation. The circle denote median estimated by hierarchical mode, and the thick line denote 68%, and thin line denote 95% posterior credible intervals. Abbreviations are: PD, potential desertification; LD, slight desertification; SD, severe desertification; VSD, very severe desertification.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2019.07.013.

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