

RESEARCH ARTICLE

Beta diversity diminishes in a chronosequence of desertification in a desert steppe

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Abstract

Biodiversity is a central and multifaceted concept of community ecology, but a major challenge remains in understanding the variation mechanisms of biodiversity. Two ecological phenomena are shown in beta diversity: (a) spatial species turnover in space and (b) nestedness-resultant of assemblages. Using a field experiment focusing on a desert steppe ecosystem, we show that desertification influences those two components in divergent ways depending on whether a deterministic or stochastic process is driving community composition. Desertification was a major driver of local environmental heterogeneity, which also resulted in decreased soil nutrients and led to increased turnover in a heterogeneous environment; however, spatial turnover of species decreased with desertification intensify. Desertification decreases resource availability, which causes species loss and reduced total beta diversity. Those desertification effects, therefore, had a homogenizing effect on the community. However, stochastic processes cannot be disregarded as a factor in community composition determination. Overall, these results indicated that the study of desertification effects on beta diversity would add our knowledge of the deterministic and stochastic processes that create and maintain biodiversity. This is crucial to assess the relative importance between stochastic processes and deterministic processes.

KEYWORDS

beta-diversity, dispersal limitation, environmental filtering, nestedness-resultant, spatial species turnover

1 | INTRODUCTION

Biodiversity is a central and multifaceted concept of community ecology, but a major challenge remains in understanding the variation mechanisms of biodiversity understand (Meiners, Cadotte, Fridley, Pickett, & Walker, 2015; Segre et al., 2014). This issue is the focus on determining which is more important in influencing species composition: deterministic processes and stochastic processes (Dini-Andreote, Stegen, van Elsas, & Salles, 2015; Li et al., 2016; Segre et al., 2014). The traditional view suggests that the deterministic process is a major driving factor in determining species diversity variation, strongly driven by biotic or abiotic factors, or a combination of both (Connell & Slatyer, 1977; Huston & Smith, 1987), and resource availability (Drury & Nisbet, 1973). However, there is an increasing awareness of the importance of stochastic processes (which means one thing occur cannot be predicted) in the variation in mechanisms of species diversity, such as sampling effects (Kraft et al., 2011; Li et al., 2016; Myers et al., 2013), local stochastic processes due to ecological drift

(Cottenie, 2005; Legendre et al., 2009), and uncaptured environmental factors and spatial variables (Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004; Myers et al., 2013). Deterministic perspectives hold that successional changes are directional, communities converge towards an adaptable environment, and a community of specialized species adapt to a local habitat. (Anderson, 2007; Lepš, 1987). In contrast, under the stochastic perspective, communities should remain divergent and no distinct single stable state of these communities is necessarily associated with resource availability (Kraft et al., 2011; Li et al., 2016; Myers et al., 2013).

Although the comparison of variations in species composition has a much longer history, the term beta diversity (β -diversity) was first introduced by Whittaker (Whittaker, 1960) and defined it as "the extent of change in community composition among sites." Whittaker (1960) went on to further state that β -diversity would establish basic knowledge about the processes that assess species diversity (Anderson et al., 2011; Chase, 2010; Kraft et al., 2011; Li et al., 2016; Myers et al., 2013; Segre et al., 2014). Therefore, β -diversity

can be used not only compares alpha diversity with gamma diversity at different scales (Baselga, 2010) but also as a measure that compares how communities respond to climate change (Baselga, 2010; Condit et al., 2002; Leprieur et al., 2011), anthropogenic interference (De Cáceres et al., 2012; Passy & Blanchet, 2007), and environmental gradients (Anderson et al., 2011; Cottenie, 2005; Myers et al., 2013).

Dissimilarity derived from the spatial turnover and dissimilarity derived from nestedness-resultant can be reflected by β -diversity (Baselga, 2007, 2010; Harrison, Ross, & Lawton, 1992). Species assemblages are considered nested when communities within species-poor sites are subsets of the species-rich sites (Ulrich & Gotelli, 2007). Contrary to nestedness-resultant components, spatial turnover occurs when some species are replaced by others (Qian, Ricklefs, & White, 2005). Although both nestedness-resultant and spatial turnover components can lead to different composition of communities among sites, their relative importance were not the same due to the difference of the ecological processes and communities structure (Brendonck, Jocqué, Tuytens, Timms, & Vanschoenwinkel, 2015; Gianuca, Declerck, Lemmens, & De Meester, 2016; Hill, Heino, Thornhill, Ryves, & Wood, 2017). Hence, partitioning β -diversity into nestedness-resultant and spatial turnover and then combining such patterns with community drivers would make us further understanding the processes that impact species diversity patterns across different sites (Baselga, Orme, Villegger, De Bortoli, & Leprieur, 2012; Ewers et al., 2013; Hortal et al., 2011; Leprieur et al., 2011). Previous studies on animal communities have focused on partitioning β -diversity (see Brendonck et al., 2015; Ewers et al., 2013; Gianuca et al., 2016; Hill et al., 2017; Hortal et al., 2011; Leprieur et al., 2011); however, none on partition β -diversity for plant communities (Si et al., 2017).

To a large extent, land degradation is caused by desertification in arid and semiarid regions (Verón & Paruelo, 2010). Both wind erosion and overgrazing are the major drivers of desertification (Deng, Zhang, & Shangguan, 2014; Li, Liu, & Wang, 2004; Tang et al., 2016). Wind erosion decreases the nutrition-rich fine sand and leads to soil impoverishment, which accelerates the progress of desertification (Tang et al., 2016). Overgrazing seriously reduces productivity of desert steppe and this leaves soil expose to outside, which increasing the probability of soil erosion and desertification (Deng, Shangguan, Wu, & Chang, 2017). A significant consequence of this stressor is the rapid reduce of species diversity in desert steppe ecosystems (Ulrich et al., 2014; Xu et al., 2015). This reduction of species diversity leads to species homogenization, which means that unique endemic species replace widespread species (Gámez-Virués et al., 2015). Species homogenization occurs in two directions: (a) distribution range expansions of non-native species and (b) distribution range contractions of native species (Olden, Poff, Douglas, Douglas, & Fausch, 2004). Species homogenization is not a new topic in community ecology research. Recently, researchers have accelerated the study of these processes and mechanisms. For example, species homogenization often occur when land-use intensification (Gossner et al., 2016). Agricultural intensification and grazing also promote species homogenization (Gámez-Virués et al., 2015; Gossner et al., 2016). Desertification leading to biodiversity loss has serious effects on function and services of desert steppe ecosystem (Chen et al., 2016; Gossner et al., 2016). However, a new challenge is that there is little knowledge about the mechanism

of species homogenization in the context of desertification. Species homogenization means a decrease in β -diversity (Gossner et al., 2016); therefore, examining the effects of desertification intensification on different components of β -diversity is critical to identifying the multiple underlying mechanisms of species homogenization.

A null model can be used for comparing the deterministic pattern to the pattern present in random matrices of the community in the context of maintaining the species occurrence frequency among local species and species richness among study sites (Gotelli, 2000). We use a null model that generates random species assemblages from the species pool to examine the relative importance of deterministic versus stochastic processes in species diversity in this study. We hypothesize that (a) desertification decreases β -diversity and spatial turnover of species leading to species homogenization; (b) deterministic processes play a dominant role in promoting species homogenization, but stochastic processes cannot be disregarded as a factor in community composition determination with desertification.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted the study in Yanchi County (elevation 1,450 m, 37°–38°N and 106°–107°E). This region is characterized by a semiarid temperate continental monsoon climate, and the mean annual temperature is 8.1 °C. In addition, the hottest weather (monthly mean temperature are 22 °C) and coldest weather (monthly mean temperature are 22 °C) usually appear in January and January. Yanchi County is a windy region with a mean annual wind speed of 2.8 m s⁻¹. There are many different soil types, such as loess, sierozem, and orthi-sandic entisols, all of which easily eroded by wind. The predominant vegetation in the study area are *Agriophyllum squarrosum* (L.) Moq., *Corispermum hyssopifolium* L., *Artemisia scoparia* Waldst. et Kit., *Leymus secalinus* var. *secalinus*, *Pennisetum centrasiacicum* Tzvel., *Salsola collina* Pall., and *Cleistogenes gracilis* Keng.

2.2 | Experimental design

The study design employed space-for-time substitution techniques. Four study areas were randomly chosen based on criteria described by Li, Jia, and Dong (2006): (a) potential desertification (considered the control), (b) slight desertification (LD), (c) severe desertification (SD), and (d) very severe desertification (VSD). Potential desertification was nondegraded steppe with cover more than 70%. LD was fixed dune with cover 50–70%. SD was semimobile dune with cover 10–50%. VSD was mobile dune with cover less than 10% (Figure 1).

Within each sampling area, four study sites were selected with the same elevation and precipitation and that exceeded 50 × 50 m dimensions (approximately 0.2 km away from one another). We randomly established three 4 × 4 m plots at the center of each study site. Then we established a 1 × 1 m quadrat at the center of each plot by fixing one polyvinyl chloride pipe in each corner of the plot for community investigation.

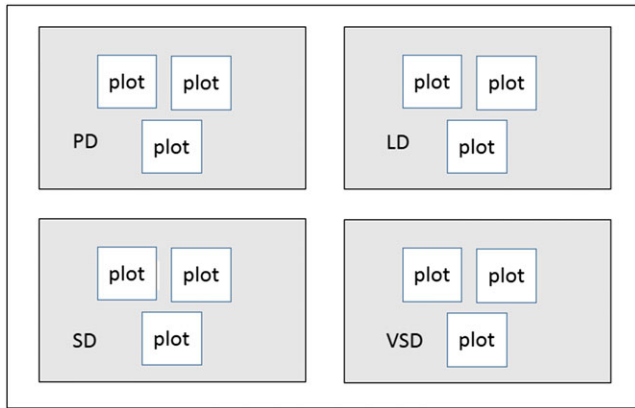


FIGURE 1 Illustration of experimental design. Abbreviations are as follows: LD = slight desertification; PD = potential desertification; SD = severe desertification; VSD = very severe desertification [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Community and soil measurement

Field surveys were performed monthly from the 25th to 30th of May, June, July, and August in 2015 and 2016. In the 1×1 m quadrat that we established at the center of each plot, plant species and richness were recorded every month. The species and number of plants were investigated. Table 1 showed the community characteristics of steppes in different desertified stage. Using a second nearby 1×1 m quadrat for destructive sampling, we cut the aboveground structures of all green plants and bring back to the lab dried for 30 min at 105°C with oven and then all the samples were oven-dried at 65°C before being weighed. Total dry biomass of every species was recorded.

Within each 1×1 m quadrat, soil samples of 0–20 cm depths were collected at three point along the diagonal, were mixed as one composite sample, and were removed plant materials and dried at room temperature. Soil moisture content was measured by each soil layer (0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, and 90–100 cm), then the mean 0–100 cm value was calculated. And soil bulk density (SB) of 0–10, 10–20, 20–30, and 30–40 cm soil layer were also measured with three replicates for each sample. The dry mass of each soil sample were measured after oven-drying at 105°C and its original volume was also measured. Considering that SB density below 40 cm is invariable, we used the mean value of SB density (0–40 cm) to conduct analysis in this research.

The wet oxidation method (Nelson & Sommers, 1982) was used to measure soil organic carbon content (SOC). The Kjeldahl acid-digestion method was used to measure soil total nitrogen content (TN). And the molybdenum blue colorimetric method was used to measure total

phosphorus content (TP) of soil with a UV/visible spectrophotometer (UV-2450/2550, Japan). We used the laser particle analyzer (operates over a range of 0.02–2,000 μm) to determine particle size.

2.4 | Statistical analyses

We quantified β -diversity using an incidence-based metric the Jaccard's dissimilarity. To examine whether β -diversity was influenced by desertification, we partitioned β -diversity into nestedness-resultant and spatial species turnover components by calculating the amount of each components input towards parts the total amount of β -diversity (Baselga, 2010). The “betapart” package was used to compute nestedness-resultant and spatial turnover in R (Baselga et al., 2012).

Our objective was to compare the observed and predicted β -diversity and to quantify the variation in observed and randomly generated spatial turnover and nestedness-resultant under random (stochastic) species replacement and species loss produced from the null models. A null-model which depending on swap algorithm was utilized to compare the expected values from null modes to the observed values (Gotelli, 2000; Ulrich & Gotelli, 2007). The swap algorithm can maintain (a) constant species richness within each community; (b) constant species occurrence frequency among communities. It also simulated species compositions through randomly sampling in each plot from the local species pool (Li et al., 2016). We obtain a null distribution of β -diversity after procedure was iterated 999 times and thus the associated spatial species turnover and nestedness-resultant components for each plot. Null modeling was performed using the “vegan” package in R (Oksanen et al., 2015).

We examined on differences in observed value (observed spatial species turnover, observed nestedness-resultant, and observed β -diversity), when compared to expected value (expected spatial species turnover, expected nestedness-resultant, and expected β -diversity), and also across environmental variables among different desertification stages. This was completed using linear mixed models (“nlme” package; Pinheiro, Bates, DebRoy, & Sarkar, 2014) to examine the influences of desertification on all of the variables. Because the study design employed space-for-time substitution techniques, so we regard the four times surveys as four times repetitive. Meanwhile, different desertification stages as fixed effect and plot as a random factor.

Then we visualized the relationships among the environmental variables in relation to plots across the four sites used generalized canonical discriminant analyses. Last, redundancy analysis (RDA) was used to calculate the variation in the observed spatial species turnover, observed nestedness-resultant, observed β -diversity, expected

TABLE 1 Community characteristics of steppes in different desertified stage

Desertified stage	PD	LD	SD	VSD
Shannon–Wiener index	1.55 ± 0.67a	1.50 ± 0.45a	1.29 ± 0.33a	0.18 ± 0.18b
Richness index	23.07 ± 0.71a	13 ± 0.71b	9.0 ± 1.41c	2.0 ± 0.01d
Aboveground biomass (g m^{-2})	80.4 ± 7.78a	58.35 ± 8.26b	28.43 ± 1.35c	4.25 ± 0.77d

Note. Value = mean ± SE, different letters indicate significant difference among different desertification stages at 0.05 level; abbreviations are as follows: LD = slight desertification; PD = potential desertification; SD = severe desertification; VSD = very severe desertification.

β -diversity, expected spatial species turnover, and expected nestedness-resultant. We used the “candisc” package to perform generalized canonical discriminant analyses (Friendly, Fox, & Friendly, 2013) and the “vegan” package to perform RDA in R (Oksanen et al., 2015).

The initial analyses included eight environmental variables. (Soil moisture content, SOC, TP, TN, SB density, clay content, silt content, and sand content). In order to avoid collinearity among environmental factors, the variables that were closely correlated with other variables were removed from the set of all environmental variables ($r > 0.80$, Figure S1), yielding four environmental variables (SOC, TP, SB density, soil moisture content) for the RDA.

3 | RESULTS

Desertification significantly decreased the observed β -diversity, which suggests that desertification leads to species homogenization. We found a larger effect from desertification on spatial turnover than on nestedness-resultant components and observed that spatial turnover significantly decreased with increasing levels of desertification ($p < .05$). In contrast, the observed nestedness-resultant components increased nonsignificantly with intensifying desertification, except in the VSD stage. Moreover, the trends in expected value was similar to the trends in observed value (Table 2).

The soil sand content of the steppes increased significantly ($p < .05$), however, clay and silt sand content decreased significantly ($p < .05$) with desertification. As desertification intensified, SB increased significantly ($p < .05$) as desertification intensified except in the LD stage. Soil moisture content is low in desert steppe ecosystems, and the maximum value of soil moisture content occurred in the LD stage, and the minimum appeared in the VSD stage. As desertification

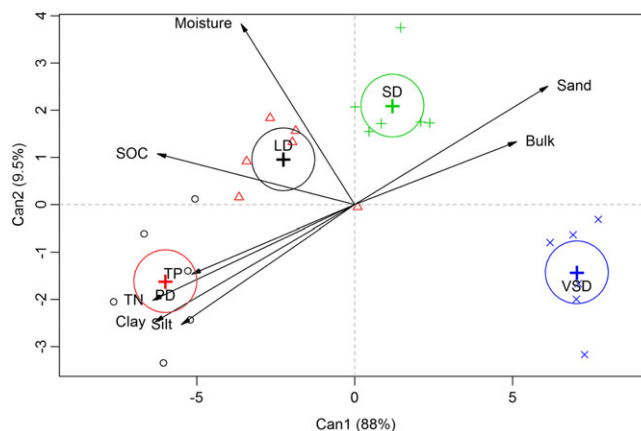


FIGURE 2 Generalized canonical discriminant analysis indicating the influence of soil variables on relationships among the different desertification stages. The circles represent the 95% confidence interval. Abbreviations are as follows: LD = slight desertification; PD = potential desertification; SD = severe desertification; SOC = soil organic carbon; TN = total soil nitrogen; TP = total soil phosphorus; VSD = very severe desertification [Colour figure can be viewed at wileyonlinelibrary.com]

intensified, SOC, TN, and TP decreased quickly along the gradient of steppe desertification (Table 2; Figure 2; $p < .05$).

To assess which is more important between deterministic and stochastic processes on patterns of nestedness-resultant components, spatial turnover, and total β -diversity, we compared the variation in the observed value components to expected value from a null model. The total variation in the observed β -diversity explained by the environmental factors was higher than the expected β -diversity (Figure 3). However, the total amount of variation in both the observed value of nestedness-resultant and spatial turnover components was lower than the expected value of them (Figure 3).

TABLE 2 Results of linear-mixed modeling for effects of desertification on variables

Variables	AIC/BIC	Intercept	Strength and direction of the desertification effect		
			LD	SD	VSD
Turnover (O)	8.44/16.44	0.64 ± 0.070 **	-0.48 ± 0.093 **	-0.24 ± 0.093 **	-0.38 ± 0.093 **
Turnover (E)	-10.33/-2.34	0.58 ± 0.051 **	-0.41 ± 0.063 **	-0.23 ± 0.063 **	-0.34 ± 0.063 **
Nestedness-resultant (O)	-15.85/-7.86	0.05 ± 0.045	0.10 ± 0.063	0.10 ± 0.063	0.21 ± 0.063 **
Nestedness-resultant (E)	-53.75/-45.75	0.11 ± 0.024 **	0.05 ± 0.028	0.11 ± 0.028 **	0.19 ± 0.028 **
Beta diversity (O)	-7.93/0.06	0.68 ± 0.052 **	-0.38 ± 0.070 **	-0.14 ± 0.070 *	-0.17 ± 0.070 **
Beta diversity (E)	-6.78/1.21	0.69 ± 0.053 **	-0.36 ± 0.071 **	-0.13 ± 0.071	-0.15 ± 0.071 *
SOC	-30.08/-24.11	0.33 ± 0.031 **	-0.09 ± 0.040 *	-0.11 ± 0.040 *	-0.29 ± 0.040 **
TN	-140.32/-134.34	0.04 ± 0.003 **	-0.01 ± 0.002 **	-0.02 ± 0.002 **	-0.03 ± 0.002 **
TP	-144.00/-138.03	0.03 ± 0.002 **	-0.01 ± 0.002 **	-0.01 ± 0.002 **	-0.01 ± 0.002 **
Soil bulk density	-55.05/-49.07	1.47 ± 0.018 **	0.02 ± 0.02	0.02 ± 0.021 **	0.02 ± 0.021 **
Moisture content	22.46/28.43	3.22 ± 0.690 **	0.43 ± 0.133 **	0.31 ± 0.133 *	-1.17 ± 0.133 **
Clay	54.54/60.51	4.32 ± 0.465 **	-1.89 ± 0.316 **	-2.85 ± 0.316 **	-3.53 ± 0.316 **
Silt	28.08/34.05	1.75 ± 0.321 **	-0.80 ± 0.160 **	-1.15 ± 0.160 **	-1.36 ± 0.160 **
Sand	70.42/76.39	93.93 ± 0.782 **	2.69 ± 0.467 **	4.00 ± 0.467 **	4.90 ± 0.467 **

Notes: The values represent the strength of the desertification effect gauged by the slope of the relationship. Positive values indicate increased, and negative values indicate decreased traits in different desertification stages. Value = slope ± SE with an asterisk indicating $p < .05$ and two asterisks indicating $p < .01$; PD as control. Abbreviations are as follows: AIC = Akaike information criterion; BIC = the Schwarz's Bayesian information criteria; E = expected value from null model; O = observed value; SOC = soil organic carbon; TN = total soil nitrogen; TP = total soil phosphorus.

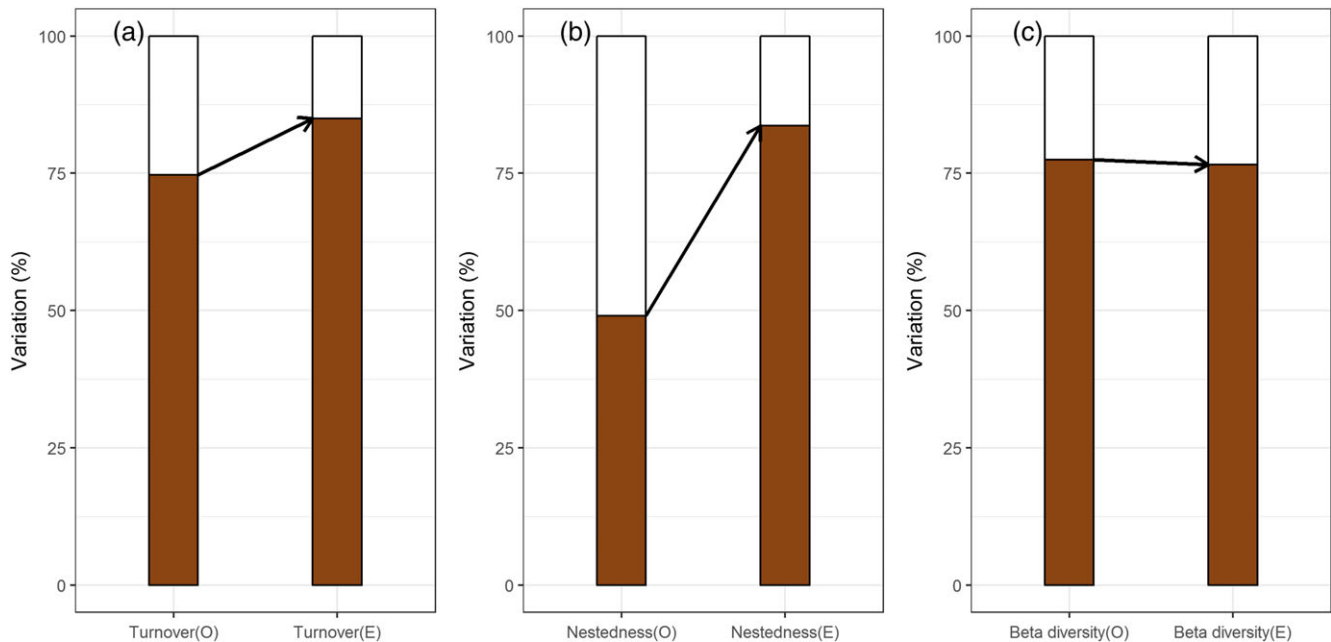


FIGURE 3 Beta diversity explained by environmental variables in the desert steppe. (a) Variation in observed turnover and expected turnover from the null-model explained by the RDA. (b) Variation in observed nestedness-resultant and expected nestedness-resultant components from the null-model explained by the RDA. (c) Variation in observed total β -diversity and expected total β -diversity from the null-model explained by the RDA. The arrows indicate the increase/decrease in the variation explained after accounting for random sampling effects. Abbreviations are as follows: E = expected value from the null model; O = observed value; RDA = redundancy analysis [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

The results of our experiment demonstrate that desertification reduces local species diversity and results in species homogenization. The community species' β -diversity could mostly be due to spatial turnover (species replacement from one site to another; Baselga, 2010) with intensifying desertification. This indicates that with intensifying desertification, variations in community composition are mainly caused by differences in species composition, rather than differences in species richness, that is, nestedness-resultant components (Viana et al., 2016). In this study, environmental factors were major causes of changing in nestedness-resultant and spatial turnover components and total β -diversity and significantly accounted for more of the variance. However, the results also show that stochastic processes that have significant effects on the spatial turnover components should not be overlooked.

The results show that desertification was a major negative driver of local environmental heterogeneity resulting in decreased soil nutrients. Additionally, desertification resulted in high spatial turnover of species among sites, which indicates that niche-selective forces are the major driving factor among species communities among different deserted sites (Gianuca et al., 2016; Segre et al., 2014; Viana et al., 2016). Species diversity decreased with desertification intensifying, and community composition reached a steady state in the condition of suitable habitat. On one hand, more habitat types can potentially support greater species variety, leading to a higher turnover component in a heterogeneous environment; however, turnover decreases with desertification intensifying. On the other hand, desertification decreases resource availability, which causes species loss. It is possible that only the species that are adapted to poor site conditions can survive and become dominant with desertification intensification.

Therefore, species homogenization occurs through loss of rare or specialized species, and frequently in combination with widespread generalist species gains (Figure 4; Gámez-Virués et al., 2015; Gossner et al., 2016; Karp et al., 2012; Smart et al., 2006).

Previous studies have also similarly demonstrated that environmental gradients affected the species replacement mainly through changing nutrient gradients (Gianuca et al., 2016; Gossner et al., 2016). Conversely, dispersal limitation plays an important role in influencing spatial turnover of species. Species would select suitable environmental conditions where dispersal is favorable within heterogeneous environments, which can increase the importance of species replacement. However, in homogeneous environments, the pattern of nestedness-resultant components would be erased when dispersal increased, which may affect species assemblages (Gianuca et al., 2016). That pattern is suggestive of desertification promoting community divergence in heterogeneous environments.

Our results also suggest that ecological processes related to habitat dispersal and filtering shape heterogeneous communities (Gianuca et al., 2016; Shurin, 2001; Spasojevic, Copeland, & Suding, 2014), which can form different species communities through species replacement along disturbance gradients. Environmental factors were the major drivers of variation in species diversity, however, it should be acknowledged that combining deterministic (i.e., habitat filtering) and stochastic processes should most effectively explain variations among vegetation communities (Myers et al., 2013; Qian et al., 2005).

This study also clearly indicates that stochastic replacement plays an important role in influencing spatial turnover of species, which is consistent with our null expectation. Initially, we found that the explained variance for spatial turnover and nestedness-resultant components by measured environmental variables were 74.7% and 49%, respectively;

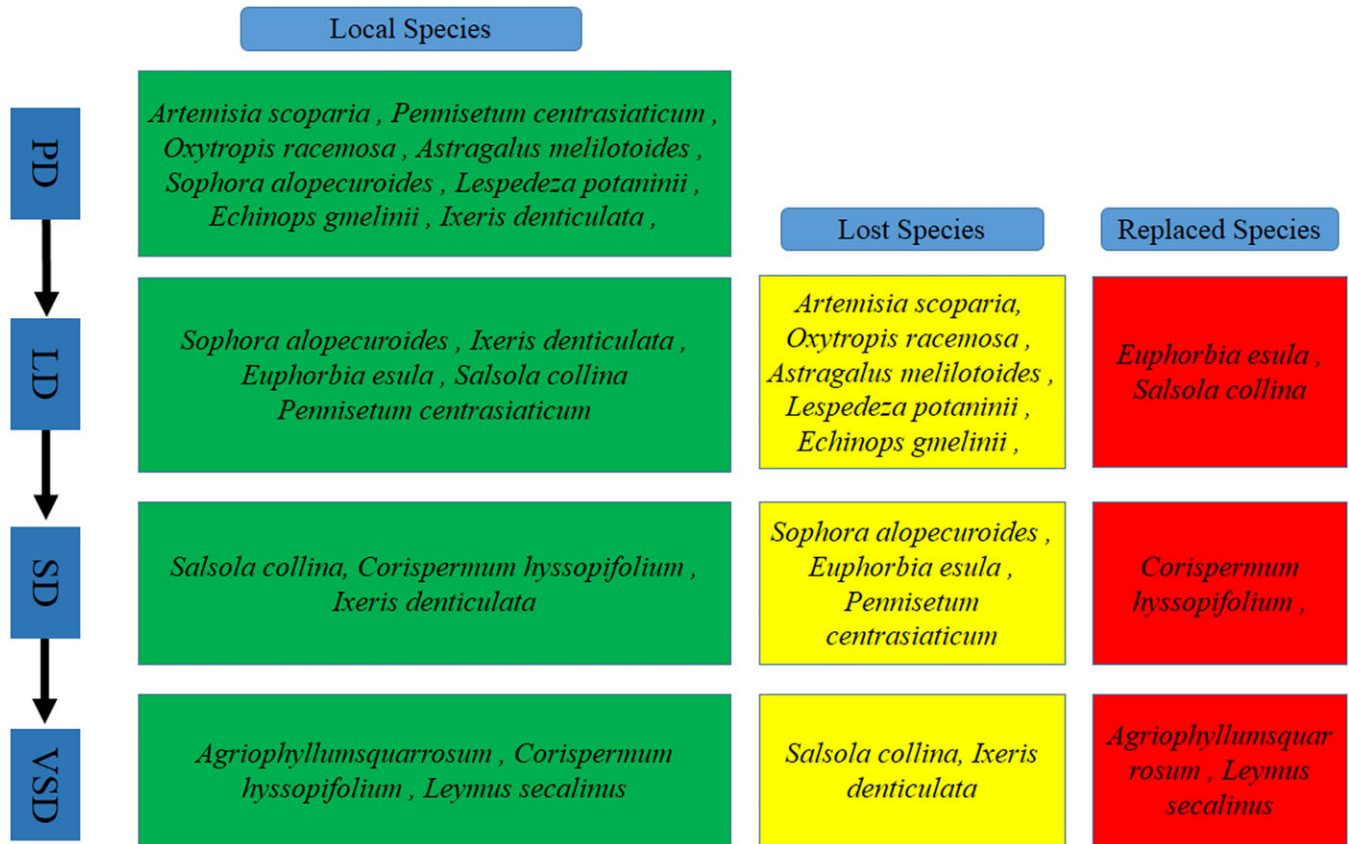


FIGURE 4 Pattern of species turnover and nestedness-resultant components with desertification development. Green rectangle, species assemblages of different desertification stage; yellow rectangle, lost species with desertification; red rectangle, replaced species with desertification. LD = slight desertification; PD = potential desertification; SD = severe desertification; VSD = very severe desertification [Colour figure can be viewed at wileyonlinelibrary.com]

however, our analysis shows that explained variation increases after take the random species assemblages effect with the null model into consideration. This finding is consistent with the results of many previous researches that used a null model and demonstrated that stochastic processes play an unavoidable role in influencing β -diversity (Kraft et al., 2011; Li et al., 2016; Myers et al., 2013). It is possible that the unexplained variance by environment may be influenced by sampling effects (Chase & Myers, 2011; De Cáceres et al., 2012), local stochastic processes due to ecological drift (Cottenie, 2005; Kraft et al., 2011; Legendre et al., 2009), and unmeasured spatial or environmental factors (Borcard et al., 2004; Myers et al., 2013). Most previous studies do not directly compare the relative importance of deterministic against stochastic processes on species composition within heterogeneous environments. However, for a few of the variables (e.g., TP, TN, clay content, silt content, and sand content, see Myers et al., 2013), the results observed in other studies are consistent with these findings. For example, Myers et al. (2013) found that soil variables play an important role in tropical tree community composition. Additionally, Gilbert and Lechowicz (2004) research showed a significant influence of environmental variables on β -diversity in a temperate forest understory.

Unexplained variation in spatial turnover, nestedness-resultant components, and total β -diversity reflect the combination of several factors: (a) sampling effects because of variations in the sizes of local species pools among different sites (Kraft et al., 2011; Li et al., 2016; Segre et al., 2014), (b) stochastic processes (e.g., extinctions and ecological drift;

Legendre et al., 2009; Segre et al., 2014), and (c) unmeasured variables (e.g., spatial/environmental factors; Borcard et al., 2004; Myers et al., 2013). Even though a majority of the variance can be explained by environmental factors, after take the sampling effects within the null model into account, the result showed that total explained β -diversity variation decreased. These results show the overall importance of deterministic processes may be overestimated relative to stochastic processes through raw comparisons of observed total β -diversity among different sites with different community assemblages.

Although the observed patterns in deterministic processes and stochastic processes are accord with our predictions, there are several limitations to this research should be noted. First, this study focused on chronosequences and inferred temporal trends from different sites at varying stages of desertification. Future studies integrating long-term community composition monitoring can help understand desertification processes. Second, this study examined a desert steppe ecosystem and cannot be extrapolated generally across all ecosystems; future studies in different ecosystems are required to gain additional insight into generalized processes underlying plant community assembly. Third, although multiple ecological processes can drive community structure, this study chiefly examined environmental variables. Future research combining long-term monitoring and environmental variables across space would provide stronger evidence to gain additional insight into the processes underlying mechanisms of plant community assembly.

In conclusion, our findings provide strong evidence that desertification intensification affects β -diversity, with ecological processes determining the specific trends. Desertification decreased the nutrition-rich fine sand leading to soil impoverishment, which accelerated the expansion of desertification and increased the habitat heterogeneity. In addition, desertification significantly decreased β -diversity among communities and led to species homogenization. A decrease in the spatial turnover component of β -diversity was likely a major factor causing homogenization under desertification. Desertification was a major driver of local environmental heterogeneity resulting in decreases in soil nutrient, which led to deterministic processes playing a larger role in determining β -diversity. However, stochastic processes cannot be disregarded in determining community composition. Baselga's method disassembles the contribution of nestedness-resultant and spatial turnover to β -diversity patterns and provides a unified framework to assess β -diversity. Therefore, the underlying mechanism of reduced β -diversity caused by desertification provides a unique method to understand the underlying process in community composition with desertification, which may provide important information to combat desertification. Thus, conservation strategies will increase in effectiveness to maintain species diversity through intensifying protection and management to prevent the desertification, such as enclosures and grazing prohibitions, rotational or seasonally grazing, increasing of soil fertility through reasonable measures of fertilizations, and others, to reduce steppe degradation, and increase biodiversity.

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SUPPORTING INFORMATION

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