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DIVERSITY–PRODUCTIVITY TRADE-OFF DURING CONVERTING CROPLAND TO PERENNIAL GRASSLAND IN THE SEMI-ARID AREAS OF CHINA

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ABSTRACT

The trade-off between plant community structure and function is an important issue during grassland restoration. It is essential to assess changes of structure and function after converting farmland to grassland. Three restoration stages (5, 15, and 30 years) were studied to determine the optimum time when the trade-off between diversity and productivity occurs. The results showed that the vegetation coverage, height, and productivity significantly increased, but the species richness, diversity, and density significantly decreased along the restoration time. Grassland community presented a succession from small individuals and high density to larger individuals and lower density. The community changed from being dominated by grass and forb functional groups to being dominated only by the grass functional group. The dominant grass functional group plays a decisive role on community structure and function (productivity, diversity, and density) during grassland succession. Our results suggest that community structure and function were mainly driven by the dominant grass functional group during the long-term succession. Grassland should be utilized to suppress the leading role of the dominant functional groups in the 20th year for keeping the trade-off of diversity and productivity. We suggest that the restoration grassland should be considered to use appropriately in the 20th year. Our study could provide a key guidance for maintaining the community structure and function trade-off for cropland-converted grassland management in the semi-arid areas.

KEY WORDS: community structure; diversity and productivity; grassland conversion; plant functional group; succession

INTRODUCTION

Global climate change, human disturbance, and desertification have resulted in a continuing serious degradation of the grassland ecosystems, such as the reduction of biodiversity and productivity (Oba *et al.*, 2008; Végvári *et al.*, 2016) and ecosystem service provision and function (Sala *et al.*, 2000; Jafari & Bakhshandehmehr, 2016; Liu *et al.*, 2016). Recent decades, increasingly ecological engineering activities are being implemented for the protection and restoration of grassland in China, including grazing exclusion (Dong *et al.*, 2008; Wu *et al.*, 2009; He *et al.*, 2011), converting cropland to grassland (Deng *et al.*, 2013), grassland establishment (Dong *et al.*, 2003; Shang *et al.*, 2008; Hu *et al.*, 2016), and other grassland management practices (Chen *et al.*, 2007; Dong *et al.*, 2010; Wang *et al.*, 2015). Meanwhile, grassland establishment is the key strategy to recover degraded soils (Taguas *et al.*, 2015; Hu *et al.*, 2016; Pereira *et al.*, 2016) and grassland management practices also influence soil habitats (Mukhopadhyay & Maiti, 2014; Parras-Alcántara *et al.*, 2015). Accordingly, understanding the ecological functions and structures of the degraded grassland is important for ecosystem restoration. An increasingly common goal of ecosystem restoration is to reconstruct the high biodiversity, productivity, and functional group diversity in general (Martin *et al.*, 2005). The loss of biodiversity may be detrimental for the ecosystem goods and services (Hector *et al.*, 1999). Thus, determining the relationship between biodiversity and productivity and understanding the mechanism are the major goals of community ecology (van Ruijven & Berendse, 2005). Previous studies have found that grassland restoration plays an important role in changing plant diversity (Adler & Levine, 2007), herbivore diversity (Borer *et al.*, 2014), productivity (Rajaniemi, 2003; Gillman & Wright, 2006; Cardinale *et al.*, 2007), and quantifying the evidence for the effects of biodiversity on ecosystem function and service provision (Cardinale *et al.*, 2002; Balvanera *et al.*, 2006; Adler & Levine, 2007; Valkó *et al.*, 2016). Gillman & Wright (2006) analyzed the results from 131 published studies, then showed that almost all productivity–richness relationships were positive in data sets of regional extent, and unimodal relationships were not dominant even in studies of fine grain or small spatial extent. However, some previous studies showed that unimodal relationships are typical in small and large scales (Kelemen *et al.*, 2013; Fraser *et al.*, 2015). A plant diversity experiment without legumes for 4 years also showed that a positive relationship between plant species richness and productivity emerged in the second year and strengthened with time (van Ruijven & Berendse, 2005).

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High richness enabled low-density communities to reach productivity levels otherwise seen only at high density; thus, density may alter diversity–productivity relationships in experimental plant communities (He *et al.*, 2005). The relationship between plant diversity and stability has also been reported (McCann, 2000; Tilman *et al.*, 2006; Ives & Carpenter, 2007). Reestablishing diversity and productivity have been widely recognized as a critical goal in restoration and an integral component of the ecological system.

The process of grassland restoration is a long-term and complex ecological process (Hastings *et al.*, 2007). It is related to many subjects, including ecology, soil science, geography, forestry, and agriculture (Gattie *et al.*, 2003; Hastings *et al.*, 2007). Particularly considering that the composition of grassland communities and species diversity are both controlled by many environmental factors and disturbances (Collins & Smith, 2006). Knowledge of the relative roles of competition and limitation as drivers of decreasing diversity in grasslands might be useful for management practice. Therefore, it is necessary to understand the changes in community composition under long-term restoration. If competition is the most important driver, major attention should be taken on appropriate management of the grassland, that is removing a sufficient amount of biomass at the right time (Deák *et al.*, 2011; Liira *et al.*, 2012). In addition, restoring community species diversity and ecosystem process rates have been regarded as the main objectives of restoration and vegetation improvement (Martin *et al.*, 2005). The time limitation that reaching the equilibrium of diversity and productivity is a critical topic for studies.

In this study, an ecological project to convert a large area of cropland to grassland was implemented in the semi-arid Loess Plateau of China. The following questions were addressed during the project of converting cropland to grassland: How community diversity and productivity change along the long-term restoration? How many restoration years are needed to convert croplands into grasslands in both plant diversity and primary productivity points reaching a trade-off? To answer the questions, we focused on grassland community structure and function, which contained three main components, namely, diversity, density, and productivity, and their interactions in three different succession stages grassland. We hypothesized that community structure and function changes were mainly driven by the dominant functional group. Our objective was to determine the time at which keep the trade-off of diversity and productivity in grassland restoration. We anticipated to be able to provide key implications for maintaining the community structure and function trade-off for cropland-converted grassland management on the Loess Plateau.

MATERIAL AND METHODS

Study Site

The study area was located in the Wangdonggou watershed (107°41′E, 35°14′N, 1120 m), at a field station of the Chinese Ecology Research Net in Changwu County, Shaanxi Province, China. This watershed is representative of the typical gully terrain of the Loess Plateau. Based on climate data from 1984 to 2005, the mean annual precipitation is 584 mm, of which nearly 52% occurs between July and September. The mean annual temperature is 9·1 °C. The soil is a coarse-textured dark loess soil.

Experimental Design

Based on the chronosequence of plant succession process in the area of study, we selected three abandoned farmlands, which were wheat field for many years prior to establishing the restored grassland. And, it had been used in restoration grassland that had been naturally restored for 5, 15, and 30 years, namely, RG_5, RG_{15}, and RG_{30} as three restoration treatments (Figure 1), respectively. All the grasslands allowed spontaneous recovery without any other disturbances. One plot (10 × 10 m) for each of treatments and five quadrats (1·0 m × 1·0 m) were randomly set in each sampling plot. Samples were taken in early September, when to reach the highest biomass. Total cover, productivity (dry aboveground biomass), plant density, and species richness (total number of species in the each quadrat) of grassland community were measured. The mean number of ramets in

Figure 1. The three restoration grasslands in this study (5-year restoration grasslands, A; 15-year restoration grasslands, B; and 30-year restoration grasslands, C). This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

Table I. Functional group and above-ground biomass for each species at the restoration grasslands (5-year restoration grasslands, RG_5; 15-year restoration grasslands, RG_{15}; and 30-year restoration grasslands, RG_{30})

Specie	Functional group	Above-ground biomass ($g\,m^{-2}$)		
		RG_5	RG_{15}	RG_{30}
Agropyron cristatum	GFG	99·98	28·03	22·88
Poa annua	GFG	55·77	41·81	436·82
Helictotrichon schellianum	GFG	—	224·46	—
Vicia sepium	LFG	14·84	20·26	20·29
Medicago ruthenica	LFG	—	25·12	16·80
Oxytropis racemosa	LFG	19·32	—	—
Viola verecunda	FFG	15·44	23·13	15·08
Potentilla acaulis	FFG	16·55	18·36	15·64
Artemisia sieversiana	FFG	33·80	46·68	18·72
Tripolium vulgare	FFG	22·91	24·32	—
Taraxacum mongolicum	FFG	15·17	85·26	—
Senecio scandens	FFG	15·88	19·16	—
Artemisia capillaris	FFG	14·67	19·50	—
Galium aparine	FFG	15·92	27·44	—
Polygala tenuifolia	FFG	14·68	—	—
Cirsium setosum	FFG	17·05	—	—
Sonchus oleraceus	FFG	16·28	—	—
Heteropappus altaicus	FFG	15·64	—	—
Calystegia hederacea	FFG	15·04	—	—
Galium aparine	FFG	—	27·44	—
Melica scabrosa	FFG	—	—	21·98

Note: grasses functional group (GFG), forbs functional group (FFG), and leguminous functional group (LFG). Symbol "—" show that there is no species at the grassland.

sampling plots represented the density of the plant community. To further investigate the changes in plant communities, we classified the plants in the communities into three plant functional groups: grasses functional group (GFG, Gramineous grass), leguminous functional group (LFG, Leguminous grass), and forbs functional group (FFG, other species) by the methods of Wu *et al.* (2009). The list of all species within each plant functional group was showed in Table I.

In each quadrat, all green, above-ground plant parts of each individual species were cut, collected, and put into separate, labeled envelopes. The below-ground biomass were collected from 0–100 cm soil layers in three places within each quadrant using a 9-cm diameter root auger. The majority of the plant roots from each sample were isolated by a 2-mm sieve, while the remaining fine roots were isolated by spreading the samples in shallow trays, overfilling the trays with water and allowing the outflow from the trays to pass through a 0·5-mm mesh sieve. All the samples were dried at 65 °C for 24 h and weighed to determine the dry mass. Dry weights were measured with 0·01 g accuracy.

Soil Sampling and Analysis

Soil samples were taken at five points in the quadrats of each plot near to the above-ground biomass sampling points. Litter horizons were collected in envelope before soil sampling. Soil samples were collected from (0–20 cm) soil layer using a soil drilling sampler (9 cm inner diameter). The samples within one quadrat were mixed together to make one composite sample. The composite soil samples were air-dried and passed through a 2-mm sieve, and roots and other debris were removed. Soil bulk density was measured using a soil bulk sampler with a 5-cm diameter and 5-cm-high stainless steel cutting ring at points adjacent to the soil sampling quadrats. The original volume of each soil core and its dry mass after oven-drying at 105 °C were measured (Deng *et al.*, 2013). The soil organic matter of these samples was then assayed by the vitriol acid-potassium dichromate oxidation method (Walkley & Black, 1934). Each analysis was carried out in three replications.

Relative Calculation

The species richness (*R*), Shannon–Wiener diversity index (*H*), Evenness index (*E*), and similarity coefficient (*J*) of the grassland communities were calculated using the following functions:

$$\text{Species richness}: \quad R = S$$

Table II. Description of dominant species, coverage, height and productivity (mean ± SE) for the three restoration grasslands (5-year restoration grasslands, RG_5; 15-year restoration grasslands, and RG_{15}; 30-year restoration grasslands, RG_{30})

Type	Coverage (%)	Height (cm)	above-ground biomass ($g\,m^{-2}$)	Dominant species
RG_5	58·00 ± 5·38 b	19·80 ± 1·36 c	301·88 ± 25·50 b	*Agropyron cristatum* *Potentilla acaulis* *Poa subfastigiata* *Artemisia sieversiana* *Tripolium vulgare*
RG_{15}	83·00 ± 4·06 a	34·76 ± 4·30 b	419·74 ± 51·79 a	*Agropyron cristatum* Potentilla acaulis *Poa subfastigiata* *Tripolium vulgare*
RG_{30}	94·00 ± 2·20 a	58·81 ± 3·30 a	496·28 ± 20·21 a	*Agropyron cristatum* *Potentilla acaulis* *Poa subfastigiata*

Note: Different letters in the same group mean significant difference at the 0·05 level among grasslands.

Table III. Description of soil bulk density, water content, soil carbon, and nitrogen (mean ± SE) at three restoration grasslands (5-year restoration grasslands, RG_5; 15-year restoration grasslands, and RG_{15}; 30-year restoration grasslands, RG_{30})

	RG_5	RG_{15}	RG_{30}
Litter biomass ($g\,m^{-2}$)	110·92 ± 10·44 b	124·56 ± 13·16 b	447·12 ± 53·16 a
Below-ground biomass ($g\,m^{-2}$)	869·26 ± 114·03 a	906·99 ± 81·68 a	843·06 ± 171·16 a
Bulk density($g\,cm^{-3}$)	1·37 ± 0·01 a	1·26 ± 0·02 b	1·33 ± 0·01 a
Water content (%)	22·64 ± 0·68 ab	21·65 ± 0·68 b	24·70 ± 0·53 a
Organic matter content ($g\,kg^{-1}$)	9·26 ± 0·46 b	11·20 ± 0·48 b	13·70 ± 0·67 a
Total nitrogen ($g\,kg^{-1}$)	0·69 ± 0·28 b	0·77 ± 0·20 ab	0·96 ± 0·43 a

Note: Different letters indicate significant differences at the 0·05 level among grasslands.

Shannon–Wiener diversity index:

$$H = \sum_{i=1}^{s} (Pi\text{In}Pi),$$

Evenness index:

$$E = \frac{H}{\ln S},$$

Where: S is the total number of species in the grassland community, *Pi* is the density of the *i* species, and *H* is the Shannon–Wiener diversity index.

$$\text{Similarity coefficients}: \quad J = j/(a + b - j)$$

Where: j is the number of species common to both quadrats and *a* and *b* are the number of species only in one and the other quadrat (Kerr *et al.*, 2001).

Statistical Analyses

The differences among each of the above-ground (coverage, height, productivity, and litter biomass) and below-ground properties (biomass, bulk density, water content, organic matter content, and total nitrogen) for a given restoring treatment were evaluated by One-way ANOVA to compare the results obtained from all the blocks. All data were expressed as the mean ± standard error (SE) of the samples collected for each treatment.

Plant community structure was analyzed to assess the effects of restoration. Differences in productivity, diversity, and density treatments were assessed using ANOVA. The relationships among functional productivity, community productivity (dependent factor), and functional density (independent factor) were estimated by regression analysis. The same method was used to analyze the relationship among community productivity, diversity, density, richness, evenness (dependent factor), and restoration time (independent factor). The regression equations (productivity–density and diversity–density) were used to identify the plant density with the graph intersection (solution of the equation group), then to identify the time in the regression of density and restoration time. Differences were evaluated at the 0·05, 0·01, and 0·001 levels of significance. All of the statistical tests were carried out using SPSS version 17·0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Composition and Productivity of Grassland Communities

The coverage significantly increased from RG_5 to RG_{15}, RG_{30} (Table II). Mean community height successively increased with the restoration time ($RG_5 < RG_{15} < RG_{30}$). The difference in productivity between RG_5 and RG_{15} was significant ($p < 0{\cdot}05$), but no significant difference was found between RG_{15} and RG_{30} (Table II). The dominant species in all the communities evaluated was *Agropyron cristatum*, and the main companion species were *Potentilla acaulis* and *Poa subfastigiata* in all RG. Meanwhile, the maximum indices of similarity between the RG_5 and RG_{15} and the RG_{15} and RG_{30} were estimated to be 0·67 and 0·50, respectively.

The highest and lowest below-ground productivity values in the 0–100 cm soil layer were 906·99 ± 81·68 $g\,m^{-2}$ in the RG_{15} area and 843·06 ± 171·15 $g\,m^{-2}$ in the RG_{30} (Table III). For the litter biomass and organic matter content, RG_{30} was significantly greater than RG_5 and RG_{15} (Table III). Soil bulk density and soil water content followed $RG_{30} > RG_5 > RG_{15}$ and RG_{30} were significantly greater than RG_{15}. Soil total nitrogen showed a tendency to increase with the restoration time (Table III).

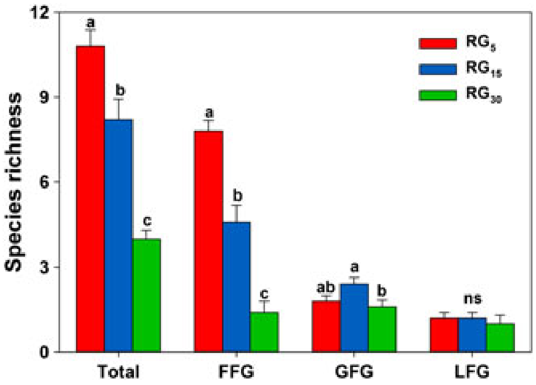

Figure 2. Community species richness and the three functional groups species richness (M ± SE) of the three restoration grasslands. RG_5, 5-year restoration grasslands; RG_{15}, 15-year restoration grasslands; and RG_{30}, 30-year restoration grasslands. GFG, grasses functional group; FFG, forbs functional group; LFG, legume functional group. Different letters in same group mean significant at the 0·05 level, ns, non-significant. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

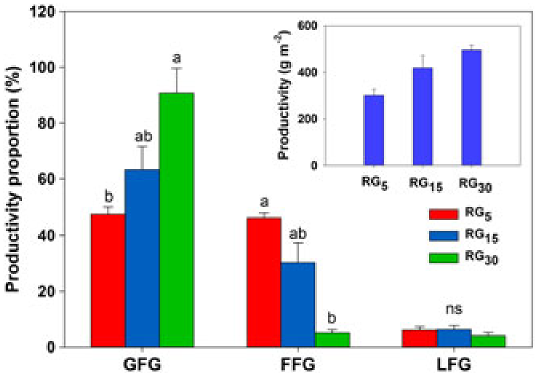

Figure 3. Community productivity and the three functional group productivity proportion (M ± SE) of the three restoration grasslands. RG_5, 5-year restoration grasslands; RG_{15}, 15-year restoration grasslands; and RG_{30}, 30-year restoration grasslands. GFG, grasses functional group; FFG, forbs functional group; LFG, legume functional group. Different letters in same group mean significant at the 0·05 level, ns, non-significant. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

Grassland Communities Plant Functional Groups and Diversity

The mean community species richness in the RG_5, RG_{15}, and RG_{30} showed significant differences ($p < 0{\cdot}05$; Figure 2). The greatest and lowest species richness were 10·8 ± 0·58 and 4·0 ± 0·31 in the RG_5 and RG_{30}, respectively. The FFG species richness had a similar variation tendency as the community species richness ($p < 0{\cdot}05$), and RG_5 had larger FFG species richness than RG_{15} and RG_{30}. However, RG_{15} had greater GFG species richness than RG_5 and RG_{30}. Meanwhile, the LFG species richness showed non-significant differences among the three grassland treatments ($p > 0{\cdot}05$). The productivity of the community and three functional groups varied significantly in response to density (Figure 3). Additionally, while the analysis of functional groups density and productivity revealed that community and GFG productivity significantly decreased with the increase of GFG density (Figure 4a,b), the relationship between the density and productivity of the community, LFG, and FFG was inconsistent (Figure 4c,d,e,f). In fact, the LFG productivity significantly increased with the increase of LFG density, whereas the community productivity decreased inversely to LFG density.

The variance of plant functional group proportion showed that the RG_{30} had significantly higher GFG and lower LFG than the RG_5 ($p < 0{\cdot}05$; Figure 3). Indeed, between the RG_5 and RG_{30} areas, the fraction of GFG productivity increased from 47·57% to 81·79%, while that of LFG productivity decreased from 46·27% to 14·54%. The LFG exhibited no significant differences among the three grassland treatments ($p > 0{\cdot}05$).

Relationship between Diversity and Productivity

Regression analysis showed that productivity significantly decreased with the increase of density, richness and evenness; nevertheless, the Shannon–Wiener index significantly increased with the increase of richness and evenness (Figure 5a,c,e). With increasing density, initially the

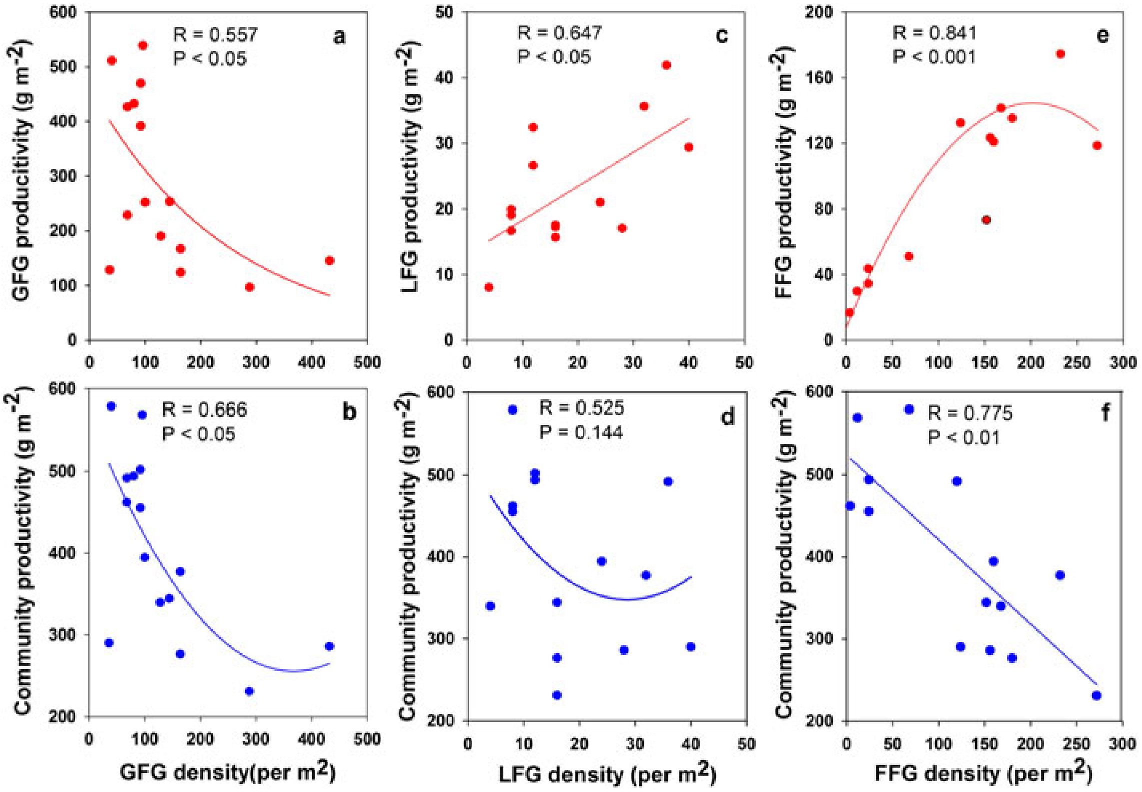

Figure 4. Relationships between three functional groups, density and the dominant functional group (grasses functional group) productivity, and total community productivity. Best-fit models based on adjusted R^2 as follows: exponential decay in panel a, linear reduction in panels c and f, and quadratic in panels b, d, and e. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

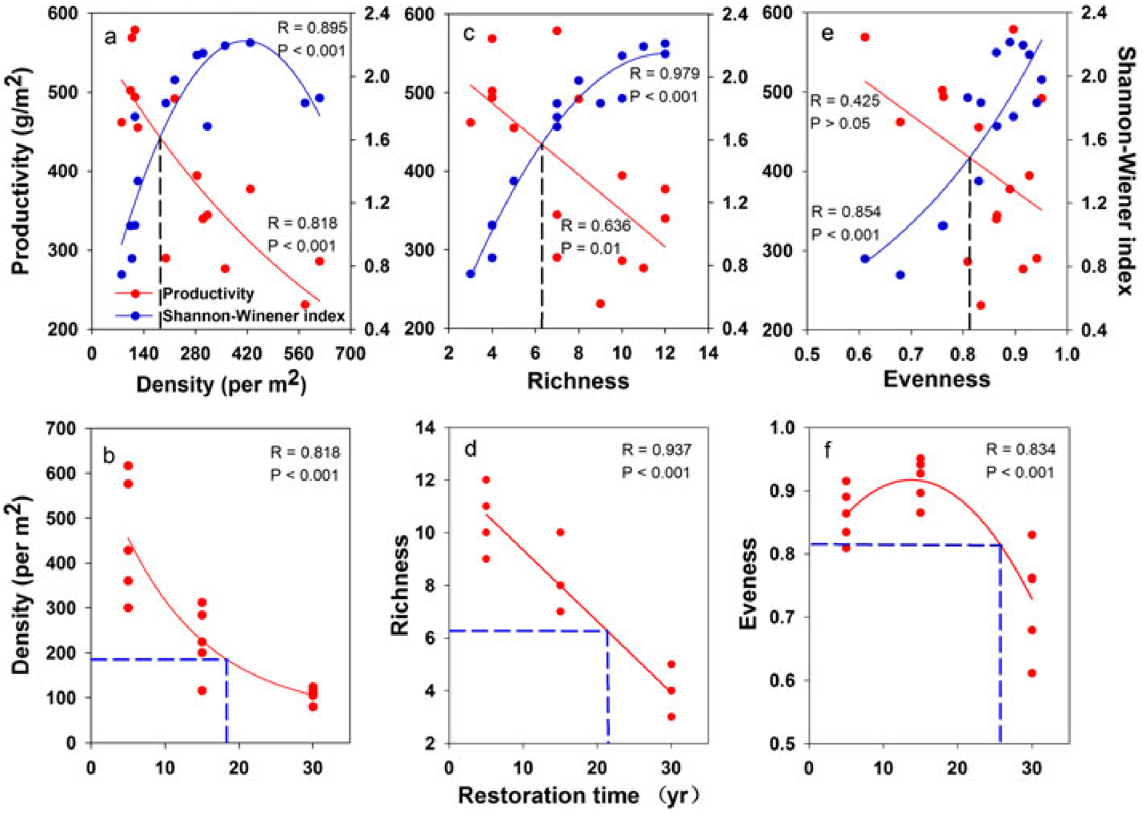

Figure 5. Variance of productivity and Shannon–Wiener with density (a), richness (c), evenness (e); effects of restoration time on the relationships between community density (b), richness (d), and evenness (f) through the restoration time period. Best-fit models based on adjusted R^2. Exponential decay of productivity and quadratic of Shannon–Wiener index with the increase of density (a); linear reduction of productivity and quadratic of Shannon–Wiener index with the increase of richness (c); linear reduction of productivity and exponential growth of Shannon–Wiener index with the increase of evenness (c); exponential decay of density (b), linear reduction of richness, (d) and quadratic of evenness (f) with increase of restoration time. The black long-dashed lines are the intersections of productivity and Shannon–Wiener index model and corresponding the fit x-axis value in panels a (the fit plant density for diversity and productivity trade-off), c (fit richness), and e (fit evenness). The values from panels a, c, and e were substituted in the model of panels b, d and f, respectively, to evaluate the fit restoration time. The fit restoration time were 18·4, 21·5, and 25·7 years for fit density, richness, and evenness (blue long-dashed lines), respectively, which determined by productivity and diversity. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

Shannon–Winener index increased until the density was about 415 plants per square meter and subsequently decreased (Figure 5a). In addition, the plant density and richness significantly decreased with the increase of restoration time (Figure 5b,d). Mean community evenness increased for the first 15 years of restoration, but subsequently declined (Figure 5f). Furthermore, the productivity showed a significant power-function increase with the restoration time ($p < 0·01$; Figure 6), but the rate of declined over time. While the diversity index showed a significant quadratic-function decrease with increasing restoration time ($p < 0·05$; Figure 6), the slope of the function decreased. Finally, the density for appropriate productivity and diversity was reached in the 19th year and estimated to be about 185 plants per square (Figure 5a); the time in the richness and evenness were 22nd (6·28) and 26th (0·81) years, respectively (Figure 5).

DISCUSSION

Our results showed that the productivity of three plant functional groups changed with the species richness and community density. The GFG productivity proportion was consistent with the variation of community productivity (Figure 2), which indicated that GFG was the dominant functional group in these grassland communities. The community composition exhibited dramatic changes because of the changes in the dominant species during long-term restoration (He *et al.*, 2011). Our results showed that above-ground productivity significantly increased after 15-year restoration, which was consistent with similar studies in other areas (Wu *et al.*, 2009; Cheng *et al.*, 2011). Moreover, with the increase of restoration time the species richness and the proportion of productivity significantly declined in the FFG, which had the highest below-ground biomass. The GFG had the highest above-ground biomass, but its below-ground biomass was relatively lower than that of the FFG. The share of FFG in community is strongly influenced by suitability of abiotic environment, availability of microsites for establishment, propagule limitation (Kelemen *et al.*, 2013). Noteworthy, the dominant GFG plays a decisive role on community structure and function (productivity, richness, diversity, and density) during grassland succession.

Species diversity decreased by the decline of the richness and density of the dominant functional group in the RG. At the initial restoration stage, high community density

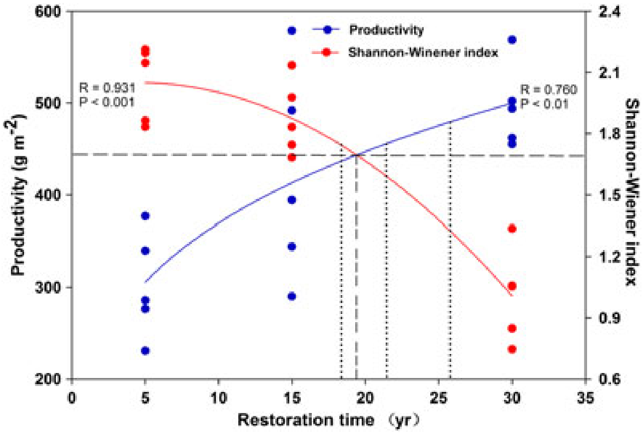

Figure 6. Relationships between grassland community productivity and species diversity through the restoration time period. Best-fit models based on adjusted R^2. Power function growth of productivity with quadratic reduction of restoration time. The black long-dashed line means the fit restoration time (19·4 years) determined by productivity and diversity trade-off. The red dotted line represented the fit restoration time from Figure 5. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr

promoted the dominance of productive species (He *et al.*, 2005). Long-term restoration resulted in lower species diversity and led to the domination of the community by a few species with strong competitive abilities (Wu *et al.*, 2009). It is generally explained by the increasing rate of competition, increasing plant size, accumulation of a thick litter layer (Kelemen *et al.*, 2013). The GFG had dominance in resource competition because of adaptive ability, such as higher height which increased light limitation (reduced transmission of photosynthetically active radiation) to other relatively lower height species (Borer *et al.*, 2014). The changes of the functional group's richness pattern result from differences in the colonization capacity and persistence of each one (Bonet, 2004). In this study, the coverage, plant height, and productivity significantly increased over time, whereas species richness, diversity, and density declined greatly. The decrease in diversity that accompanies the increase in standing crop has been explained by the intensification of asymmetric light competition (Deák *et al.*, 2011; Liira *et al.*, 2012). These results are consistent with previous result (Martin *et al.*, 2005). Previously, it was revealed that diversity loss in high-productivity grassland may result from greater competition for canopy resources, and some species with less competitive ability reduce their density or disappear because of competition for light resources or nutrients (Cheng *et al.*, 2011). It is an indirect evidence of competition as a driver of community changes, which is also offered by proportion of species traits that increasing competitive ability. The decline in richness and evenness has been attributed to the increase in biomass, height of dominant plant functional group, which resulted in light limitation (Borer *et al.*, 2014). Meanwhile, long-term grazing exclusion caused litter accumulation, which in turn affected the community structure and diversity (Liu *et al.*, 2010). Some authors suggest that accumulated litter plays a more important role in determining species richness than green biomass (Kelemen *et al.*, 2013).The botanical components in the RG_{30} indicated that the grassland underwent a change from a community with small individuals and high density to a community with larger individuals and lower density. Indeed, the grass-dominated community on the Loess Plateau was changed to a forb-dominated functional group. This finding is in agreement with a previous study in fenced alpine meadow (Wu *et al.*, 2009). It is also consistent with the result of Lin *et al.* (2015), which showed that plant functional group shifted from rhizome bunch grasses to rhizome plexus and dense plexus grasses during the degradation process in alpine meadow.

It is worthwhile emphasizing that the importance of establishing and maintaining grassland communities with high diversity of dominant species and functional groups for grassland restoration has been previously recognized (Bai *et al.*, 2004). The time elapsed since restoration has been demonstrated that it affected the species richness and composition in grassland (Tikka *et al.*, 2001; Lindborg & Eriksson, 2004; Zhang & Dong, 2010). Our study showed that long-term restoration leads to a decrease in species density, richness, and evenness. Therefore, in this study our working hypothesis has been identified involving the limits of restoration time for an effective productivity and diversity in grassland restoration. For instance, our results showed that productivity and diversity reached equilibrium after a 21-year natural restoration. This result is consistent with the results of Jing *et al.* (2013), which showed that the species diversity and biomass reached the peak values in the 20th year in continental steppe grassland. The high diversity decline was previously found to occur as a result of biomass accumulation and competition increasing (Guo, 2005). The density, richness, and evenness, integrated with both productivity and diversity, reached equilibrium on the 19th, 22nd, and 26th years, respectively. Evenness reached the peak value in approximately 15 years, and then gradually decreased. Thus, the results indicated that the rational time is a very important factor in ecological restoration and the optimum restoration time required in RG is 19–21 years.

Restoration grassland ecosystem is a complex and lengthy process, which is restricted by many biotic and abiotic factors (Cheng *et al.*, 2011; Mukhopadhyay & Maiti, 2014; Lu *et al.*, 2015; Pereira *et al.*, 2016). To evaluate the grassland restoration effect, both authropogenic and climatic impacts should be considered. Diversity and productivity changes represent the most responses of grassland to climate changes and human activities (van Ruijven & Berendse, 2005; Gong *et al.*, 2015). In some cases, the disturbances caused some changes of other factors to affect productivity and diversity (Pereira *et al.*, 2014; Parras-Alcántara *et al.*, 2015; Wang *et al.*, 2015). To maintain high-efficiency ecological and economic benefits of grassland ecosystem, the factors as many as possible should be considered in the studies. Long-term grassland restoration chronosequence in continuous and large spatial scales experiments should be conducted in the future.

CONCLUSIONS

Our results showed that long-term natural restoration increased community productivity, but significantly decreased species richness, diversity, and density. The dominant GFG plays a decisive role on community structure and function (productivity, richness, diversity, and density) during grassland succession. Grassland community showed a succession from a community with the small individuals and high density to a community with larger individuals and lower density. Grass-dominated community changed to forb-dominated one, and a new degraded one was shown after 20-year succession in the Loess Plateau. Our results suggest that changes of community structure and function were mainly derived from the dominant grass functional group during the conversion of cropland to grassland. The naturally restored grassland should be utilized to suppress the leading role of the dominant functional group before a new degradation of grassland community function. Our study provided a key implication for maintaining the community structure and function trade-off for cropland-converted grassland management on regional scale. Our study represents only three stages in a 30-year restoration chronosequence, so it is difficult to determine the change of relationship between diversity and productivity along the restoration time. Long-term and continuous experiments should be designated for studying sustainable grassland restoration management regimes in the future.

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REFERENCES

Adler PB, Levine JM. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* **116**: 221–232. DOI:10.1111/j.2006.0030-1299.15327.x.

Bai YF, Han XG, Wu JG, Chen ZZ, Li LH. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* **431**: 181–184. DOI:10.1038/nature02850.

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**: 1146–1156. DOI:10.1111/j.1461-0248.2006.00963.x.

Bonet A. 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. *Journal of Arid Environments* **56**: 213–233. DOI:10.1016/S0140-1963(03)00048-X.

Borer ET, Seabloom EW, Gruner DS, Harpole WS, Hillebrand H, Lind EM, Adler PB, Alberti J, Anderson TM, Bakker JD, Biederman L, Blumenthal D, Brown CS, Brudvig LA, Buckley YM, Cadotte M, Chu CJ, Cleland EE, Crawley MJ, Daleo P, Damschen EI, Davies KF, DeCrappeo NM, Du GZ, Firn J, Hautier Y, Heckman RW, Hector A, HilleRis Lambers J, Iribarne O, Klein JA, Knops JMH, La Pierre KJ, Leakey AD, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Mortensen B, O'Halloran LR, Orrock JL, Pascual J, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Williams RJ, Wragg PD, Wright JP, Yang LH. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**: 517–520. DOI:10.1038/nature13144.

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* **104**: 18123–18128. DOI:10.1073/pnas.0709069104.

Cardinale BJ, Harvey CT, Gross K, Ives AR. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**: 426–429. DOI:10.1038/415426a.

Chen LD, Gong J, Fu BJ, Huang ZL, Huang YL, Gui LD. 2007. Effect of land use conversion on soil organic carbon sequestration in the loess hilly area, Loess Plateau of China. *Ecological Research* **22**: 641–648. DOI:10.1007/s11284-006-0065-1.

Cheng J, Wu GL, Zhao LP, Li Y, Li W, Cheng JM. 2011. Cumulative effects of 20-year exclusion of livestock grazing on above- and belowground biomass of typical steppe communities in arid areas of the Loess Plateau, China. *Plant Soil Environment* **57**: 40–44.

Collins SL, Smith MD. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* **87**: 2058–2067. DOI:10.1890/0012-9658(2006)87[2058:SIOFAG]2.0.CO;2.

Deng L, Shangguan ZP, Sweeney S. 2013. Changes in soil carbon and nitrogen following land abandonment of farmland on the Loess Plateau, China. *PLoS One* **8**: e71923. DOI:10.1371/journal.pone.0071923.

Deák B, Valkó O, Kelemen A, Török P, Miglécz T, Ölvedi T, Lengyel SZ, Tóthmérész B. 2011. Litter and graminoid biomass accumulation suppresses weedy forbs in grassland restoration. *Plant Biosystems* **145**: 730–737. DOI:10.1080/11263504.2011.601336.

Dong SK, Long RJ, Hu ZZ, Kang MY, Pu XP. 2003. Productivity and nutritive value of some cultivated perennial grasses and mixture in the alpine region of the Tibetan Plateau. *Grass and Forage Science* **58**: 302–308. DOI:10.1046/j.1365-2494.2003.00382.x.

Dong SK, Gao HW, Xu GC, Hou XY, Long RJ, Kang MY. 2008. Farmer and professional attitudes to the large-scale ban on livestock grazing of grasslands in China. *Environment Conservation* **34**: 246–254. DOI:10.1017/S0376892907004420.

Dong SK, Li JP, Li XY, Wen L, Zhu L, Li YY, Ma YS, Shi JJ, Dong QM, Wang YL. 2010. Application of design theory for restoring the "black beach" degraded rangeland at the headwater areas of the Qinghai-Tibetan Plateau. *African Journal of Agriculture Research* **25**: 3542–3552. DOI:10.5897/AJAR10.005.

Fraser LH, Pithe J, Jentsch A, Sternberg M, Zobel M, Askarizadeh D, Bartha S, Beierkuhnlein C, Bennett JA, Bittel A, Boldgiv B, Boldrini II, Bork E, Brown L, Cabido M, Cahill J, Carlyle CN, Campetella G, Chelli S, Cohen O, Csergo AM, Díaz S, Enrico L, Ensing D, Fidelis A, Fridley JD, Foster B, Garris H, Goheen JR, Henry HAL, Hohn M, Jouri MH, Klironomos J, Koorem K, Lodge RL, Long RJ, Manning P, Mitchell R, Moora M, Müller SC, Nabinger C, Naseri K, Overbeck GE, Palmer TM, Parsons S, Pesek M, Pillar VD, Pringle RM, Roccaforte K, Schmidt A, Shang ZH, Stahlmann R, Stotz GC, Sugiyama S, Szentes S, Thompson D, Tungalag R, Undrakhbold S, van Rooyen M, Wellstein C, Wilson JB, Zupo T. 2015. Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* **349**: 302–305. DOI:10.1126/science.aab3916.

Gattie DK, Smith MC, Tollner EW, Mccutcheon SC. 2003. The emergence of ecological engineering as a discipline. *Ecological Engineering* **20**: 409–420. DOI:10.1016/j.ecoleng.2003.08.003.

Gillman LN, Wright SD. 2006. The influence of productivity on the species richness of plants, a critical assessment. *Ecology* **87**: 1234–1243. DOI:10.1890/0012-9658(2006)87[1234:TIOPOT]2.0.CO;2.

Gong Z, Kawamura K, Ishikawa N, Goto M, Wulan T, Alateng D, Yin T, Ito Y. 2015. MODIS normalized difference vegetation index (NDVI) and vegetation phenology dynamics in the Inner Mongolia grassland. *Solid Earth* **6**: 1185–1194. DOI:10.5194/se-6-1185-2015.

Guo QF. 2005. Plant communities, ecosystem maturity and performance. *Nature* **435**: E6–7. DOI:10.1038/nature03583.

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. 2007. Ecosystem engineering in space and time. *Ecology Letters* **10**: 153–164. DOI:10.1111/j.1461-0248.2006.00997.x.

He JS, Wolfe-Bellin KS, Schmid B, Bazzaz FA. 2005. Density may alter diversity–productivity relationships in experimental plant communities.

Basic and Applied Ecology **6**: 505–517. DOI:10.1016/j.baae.2005.04.002.

He NP, Han XG, Yu GR, Chen QS. 2011. Divergent changes in plant community composition under 3-decade grazing exclusion in continental steppe. *PLoS One* **6**: e26506. DOI:10.1371/journal.pone.0026506.

Hector A, Schmid B, Beierkuhnlein C, Caldeira M, Diemer M, Dimitrakopoulos P, Finn J, Freitas H, Giller P, Good J. 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127. DOI:10.1126/science.286.5442.1123.

Hu GZ, Liu HY, Yin Y, Song ZL. 2016. The role of legumes in plant community succession of degraded grasslands in northern China. *Land Degradation & Development* **27**: 366–372. DOI:10.1002/ldr.2382.

Ives AR, Carpenter SR. 2007. Stability and diversity of ecosystems. *Science* **317**: 58–62. DOI:10.1126/science.1133258.

Jafari R, Bakhshandehmehr L. 2016. Quantitative mapping and assessment of environmentally sensitive areas to desertification in central Iran. *Land Degradation & Development* **27**: 108–119. DOI:10.1002/ldr.2227.

Jing ZB, Cheng JM, Chen A. 2013. Assessment of vegetative ecological characteristics and the succssion process during tree decades of grazing exclusion in a continental steppe grassland. *Ecological Engineering* **57**: 162–169. DOI:10.1016/j.ecoleng.2013.04.035.

Kelemen A, Török P, Valkó O, Miglécz T, Tóthmérész B. 2013. Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science* **24**: 1195–1203. DOI:10.1111/jvs.12027.

Kerr JT, Southwood TR, Cihlar J. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences* **98**: 11365–11370. DOI:10.1073/pnas.201398398.

Liira J, Ingerpuu N, Kalamees R, Moora M, Pärtel M, Püssa K, Roosaluste E, Saar L, Tamme R, Zobel K, Zobel M. 2012. Grassland diversity under changing productivity and the underlying mechanisms – results of a 10-yr experiment. *Journal of Vegetation Science* **23**: 919–930. DOI:10.1111/j.1654-1103.2012.01409.x.

Lin L, Li YK, Xu XL, Zhang FW, Du YG, Liu SL, Guo XW, Cao GM. 2015. Predicting parameters of degradation succession processes of Tibetan Kobresia grasslands. *Solid Earth* **6**: 1237–1246. DOI:10.5194/se-6-1237-2015.

Lindborg R, Eriksson O. 2004. Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restoration Ecology* **12**: 318–326. DOI:10.1111/j.1061-2971.2004.00334.x.

Liu P, Huang JH, Sun OJ, Han XG. 2010. Litter decomposition and nutrient release as affected by soil nitrogen availability and litter quality in a semiarid grassland ecosystem. *Oecologia* **162**: 771–780. DOI:10.1007/s00442-009-1506-7.

Liu SB, Schleuss PM, Kuzyakov Y. 2016. Carbon and nitrogen losses from soil depend on degradation of Tibetan *Kobresia* pastures. *Land Degradation & Development*. DOI:10.1002/ldr.2522.

Martin LM, Moloney KA, Wilsey BJ. 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* **42**: 327–336. DOI:10.1111/j.1365-2664.2005.01019.x.

Lu X, Yan Y, Sun J, Zhang X, Chen Y, Wang X, Cheng G. 2015. Short-term grazing exclusion has no impact on soil properties and nutrients of degraded alpine grassland in Tibet, China. *Solid Earth* **6**: 1195–1205. DOI:10.5194/se-6-1195-2015.

McCann KS. 2000. The diversity–stability debate. *Nature* **405**: 228–233. DOI:10.1038/35012234.

Mukhopadhyay S, Maiti SK. 2014. Soil CO_2 flux in grassland, afforested land and reclaimed coalmine overburden dumps: a case study. *Land Degradation & Development* **25**: 216–227. DOI:10.1002/ldr.1161.

Oba G, Byakagaba P, Angassa A. 2008. Participatory monitoring of biodiversity in East African grazing lands. *Land Degradation & Development* **19**: 636–648. DOI:10.1002/ldr.867.

Parras-Alcántara L, Díaz-Jaimes L, Lozano-García B. 2015. Management effects on soil organic carbon stock in mediterranean open rangelands-treeless grasslands. *Land Degradation & Development* **26**: 22–34. DOI:10.1002/ldr.2269.

Pereira P, Cerdà A, Lopez AJ, Zavala LM, Mataix-Solera J, Arcenegui V, Misiune I, Keesstra S, Novara A. 2016. Short-term vegetation recovery after a grassland fire in Lithuania: the effects of fire severity, slope position and aspect. *Land Degradation & Development*. DOI:10.1002/ldr.2498.

Pereira P, Úbeda X, Mataix-Solera J, Oliva M, Novara A. 2014. Short-term changes in soil Munsell colour value, organic matter content and soil water repellency after a spring grassland fire in Lithuania. *Solid Earth* **5**: 209–225. DOI:10.5194/se-5-209-2014.

Rajaniemi TK. 2003. Explaining productivity-diversity relationships in plants. *Oikos* **101**: 449–457. DOI:10.1034/j.1600-0706.2003.12128.x.

Sala OE, Chapin IIIFS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson R, Kinzig A, Leemans R, Lodge D, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1776. DOI:10.1126/science.287.5459.1770.

Shang ZH, Ma YS, Long RJ, Ding LM. 2008. Effect of fencing, artificial seeding and abandonment on vegetation composition and dynamics of 'black soil land'in the headwaters of the Yangtze and the Yellow Rivers of the Qinghai-Tibetan Plateau. *Land Degradation & Development* **19**: 554–563. DOI:10.1002/ldr.861.

Taguas EV, Arroyo C, Lora A, Guzmán G, Vanderlinden K, Gómez JA. 2015. Exploring the linkage between spontaneous grass cover biodiversity and soil degradation in two olive orchard microcatchments with contrasting environmental and management conditions. *The Soil* **1**: 651–664. DOI:10.5194/soil-1-651-2015.

Tikka PM, Heikkila T, Heiskanen M, Kuitunen M. 2001. The role of competition and rarity in the restoration of a dry grassland in Finland. *Applied Vegetation Science* **4**: 139–146. DOI:10.1111/j.1654-109X.2001.tb00244.x.

Tilman D, Reich PB, Knops JMH. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**: 629–632. DOI:10.1038/nature04742.

van Ruijven J, Berendse F. 2005. Diversity–productivity relationships, initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences* **102**: 695–700. DOI:10.1073/pnas.0407524102.

Valkó O, Deák B, Török P, Kelemen A, Miglécz T, Tóth K, Tóthmérész B. 2016. Abandonment of croplands: problem or chance for grassland restoration? Case studies from Hungary. *Ecosystem Health and Sustainability* **2**: e01208. DOI:10.1002/ehs2.1208.

Végvári Z, Valkó O, Deák B, Török P, Konyhás S, Tóthmérész B. 2016. Effects of land use and wildfires on the habitat selection of Great Bustard (*Otis tarda* L.) – Implications for species conservation. *Land Degradation & Development* **27**: 910–918. DOI:10.1002/ldr.2495.

Walkley A, Black IA. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science* **37**: 29–38. DOI:10.1097/00010694-193401000-00003.

Wang CT, Wang GX, Wang Y, Rafique R, Ma L, Hu L, Luo YQ. 2015. Fire alters vegetation and soil microbial community in alpine meadow. *Land Degradation & Development*. DOI:10.1002/ldr.2367.

Wu GL, Du GZ, Liu ZH, Thirgood S. 2009. Effect of fencing and grazing on a *Kobresia*-dominated meadow in the Qinghai-Tibetan Plateau. *Plant and Soil* **319**: 115–126. DOI:10.1007/s11104-008-9854-3.

Zhang JT, Dong YR. 2010. Factors affecting species diversity of plant communities and the restoration process in the loess area of China. *Ecological Engineering* **36**: 345–350. DOI:10.1016/j.ecoleng.2009.04.001.