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Asymmetric effects of litter accumulation on soil temperature and dominant plant species in fenced grasslands

Dongjie Hou,[1,2] Changcheng Liu,[1,]† Xianguo Qiao,[1,2] and Ke Guo[1,2]

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093 China*
[2]*University of Chinese Academy of Sciences, Beijing 100049 China*

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Abstract. Excess litter accumulates on the soil surface of fenced grasslands and alters the abiotic environment and plant population dynamics. However, little is known about the effect of litter accumulation on the interaction between environmental factors and plant population characteristics in fenced grasslands, especially over different time scales. We applied a three-year litter removal experiment to two kinds of fenced grasslands in Inner Mongolia, China. We measured soil temperature *in situ* and plant phenology and population characteristics of three dominant species (*Stipa grandis*, *S. krylovii*, and *Leymus chinensis*). During the growing season, litter accumulation (i.e., the control) significantly decreased soil temperature, with a larger effect in the daytime than at night. The diurnal negative effect gradually weakened across the growing season, whereas the negative effect in the nighttime shifted to a positive effect on soil temperature in the late growing season. The decreased soil temperature delayed plant phenology, with longer delays in *S. grandis* and *S. krylovii* than *L. chinensis*. Litter accumulation also significantly increased the height, cover, root biomass, and relative dominance of *L. chinensis* but decreased cover, density, root biomass, and relative dominance of both *Stipa*, driving replacement of *S. grandis* or *S. krylovii* by *L. chinensis* in two grasslands. Our findings emphasize the critical function of litter in grassland management and provide a new insight to elucidating the mechanism of how litter accumulation regulates the abiotic environment, community composition and structure, and successional change in fenced grasslands.

Key words: abiotic environment; asymmetric effect; Inner Mongolia; plant phenology; population characteristics; temperate grasslands.

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† **E-mail:** greatwall01@ibcas.ac.cn

Introduction

Wilted, abscised, and decomposing plant material (i.e., plant litter) is a critical component of many arid and semiarid grasslands and often influences community composition, structure, and productivity (Wang et al. 2011, Letts et al. 2015). Plant litter acts to mediate the interactions between the abiotic environment and the plant community. Litter accumulation decreases soil temperatures (Facelli and Pickett 1991, Weltzin et al. 2005) that regulate seed germination (Eckstein and Donath 2005), plant growth (Facelli and Pickett 1991, Song et al. 2018), and the mineralization rates of soil nutrients (Weltzin et al. 2005). Litter accumulation is a mechanical barrier to heat exchange between the soil and air through two contrasting effects (Facelli and Pickett 1991, Weltzin et al. 2005). For example, in the daytime, litter shades the soil, reducing the absorption of solar radiation and keeping soil temperature lower than bare soil (Facelli and Pickett 1991, Song et al. 2018). But in the nighttime, litter prevents heat loss from soil, keeping

soil temperatures higher (Facelli and Pickett 1991, Weltzin et al. 2005). However, these two effects of litter accumulation on soil temperatures are not well understood. In addition, most previous studies of the effects of litter accumulation on soil temperatures usually integrate over the entire day (e.g., daily mean, daily maximum, and daily minimum; Song et al. 2018), neglecting the differences between daytime and nighttime soil temperatures. Furthermore, as air temperature and community characteristics change during the course of the growing season, the efficiency of these two effects could also change. Xia et al. (2010) reported that community composition, structure, and function can be altered by slight changes in soil temperature. Unfortunately, little is known about how litter accumulation regulates soil temperatures across different time scales, which is important for understanding the effects of litter accumulation on plant populations and communities.

Litter accumulation affects the plant population characteristics and interspecific relationships (Facelli and Pickett 1991) that are driving forces of community composition and structure (Ruprecht et al. 2008). For example, litter accumulation alters plant phenology via effects on soil temperature and moisture (Zhu et al. 2016). Additionally, species with different sensitivities to litter accumulation have diverse responses, in terms of aboveground and belowground morphology and population characteristics (Facelli and Pickett 1991). For instance, litter accumulation increases the cover and aboveground biomass of some species but decreases that of others (Weltzin et al. 2005, Kelemen et al. 2013). Litter accumulation also acts as a mechanical barrier, preventing seeds from reaching the soil surface (Jensen and Gutekunst 2003, Loydi et al. 2013), as well as decreasing the light quantity and quality reaching the soil (Hou et al. 2019), inhibiting germination of some species (Jensen and Gutekunst 2003). Some secondary metabolites in leaf litter also inhibit population renewal (Hovstad and Ohlson 2008, Ruprecht et al. 2008). These changes in plant phenology, form, and population dynamics further influence community composition, structure, and function (Xiong and Nilsson 1999, Amatangelo et al. 2008, Letts et al. 2015), and even productivity (Willms et al. 1993, Deutsch et al. 2010, Wang et al. 2011). Ultimately, the altered interspecific relationships under litter accumulation could drive alternate community successional trajectories (Jing et al. 2013, Hou et al. 2019).

Grassland ecosystems are one of the important terrestrial ecosystems in China, covering 40% of its land area (Kang et al. 2007). Most grasslands in China have suffered from severe degradation due to long-term overgrazing over the past decades (Kang et al. 2007, Wiesmeier et al. 2009). To restore these degraded grasslands, fencing that limits grazing is regarded as an effective and simple method, which has been widely applied in northern China and especially in Inner Mongolia (Han et al. 2009, Liu et al. 2019). Plant height, cover, aboveground biomass, and soil nutrients of degraded grasslands have been improved after long-term fencing in Inner Mongolia (Liu et al. 2017, 2019, Sagar et al. 2019). However, compared with other grassland managements (e.g., grazing and mowing), long-term fencing also results in remarkable litter accumulation on the surface of grasslands. The effects of this litter accumulation on the abiotic environment, plant population characteristics, and community structure and function are still unclear.

Bunchgrass grasslands, dominated by *Stipa grandis* or *S. krylovii*, are typical of Inner Mongolia. The species *S. grandis*, *S. krylovii,* and *Leymus chinensis* are widely distributed in these two kinds of grasslands, playing important roles in regulating interspecific relationships and community structure and productivity. However, the three species have different characteristics in terms of morphology, plant functional group, and ecological adaptations (Chen et al. 2005, Liu et al. 2018). For example, *S. grandis* and *S. krylovii* are bunch grasses with deeper roots, adapted to a relatively dry environment (Chen et al. 2005). In contrast, *L. chinensis* is a typical rhizomatous grass with long, strong rhizomes and clonal propagation (Bai et al. 2009) that grows in a relatively moist environment (Chen et al. 2005). However, there are few reports on the adaptability of these three species to litter accumulation in fenced grasslands.

The aim of this study was to examine the effects of litter accumulation on the soil temperature, plant phenology, and population characteristics of the dominant species in fenced grasslands. During 2015–2017, soil temperature

was continuously monitored and plant phenology and population characteristics of *S. grandis*, *S. krylovii*, and *L. chinensis* were investigated in two fenced grasslands in Inner Mongolia, China. We addressed the following questions: (1) How does litter accumulation regulate soil temperature at different time scales? (2) How do the three dominant species, with different ecological traits, respond to litter accumulation?

Materials and Methods

Study area

The experiment was conducted in Xilin Gol League, Inner Mongolia, China, on typical representative grasslands of this region that are dominated by one of two species of *Stipa*. The *S. grandis* grassland was located at the Inner Mongolia Grassland Ecosystem Research Station of the Chinese Academy of Sciences (43°33′37″ N, 116°40′12″ E). The *S. krylovii* grassland was located at the Grassland Ecological Research Station of Inner Mongolia University (44°09′44″ N, 116°29′08″ E). Fenced exclosures (1000 × 800 m) were established in both grasslands for five years (2009–2014). Excess litter accumulated on the surface of both sites. *L. chinensis* (Poaceae) is a subdominant species in the two grasslands, and other species includes *Cleistogenes squarrosa* (Poaceae), *Carex duriuscula* (Cyperaceae), *Potentilla tanacetifolia* (Rosaceae), and *Artemisia frigida* (Asteraceae).

In the *S. grandis* grassland, the mean annual temperature is 0.3°C, the monthly mean temperature ranges from −21.6°C in January to 19.0°C in July, and the mean annual precipitation is 351 mm. In the *S. krylovii* grassland, the mean annual temperature is 0.1°C, the monthly mean temperature ranges from −19.0°C in January to 21.4°C in July, and the mean annual precipitation is 300 mm. In both grasslands, 80% of the precipitation occurs between May and August, and the soil type is a chestnut soil (Chinese Soil Taxonomic Classification). The growing season starts in late April and lasts to mid-September in both sites.

Experimental design

A three-year field experiment was conducted during 2015–2017 with a random complete block design. Within each fenced grassland, three blocks (50 × 22 m) were established and the distance between two blocks was 200 m. In each block, the half of block (50 × 10 m) was randomly assigned as the litter removal treatment and the other half (50 × 10 m) was the control treatment, separated by a 2-m buffer. All the litter (mainly including dead, aboveground leaves, and stems of plants) in the litter removal treatment was cut near the soil surface and removed at the end of the growing season in late October 2014–2016 (Hou et al. 2019). The all litter in the control treatment was retained throughout the experiment.

Soil temperature

We continuously measured soil temperature (°C) using ECH_2O 5TE sensors (Decagon Devices, Pullman, Washington, USA). In each treatment half-block, ECH_2O 5TE sensors were installed in the soil at 2.5 cm and 12.5 cm depths. Soil temperature was automatically recorded at 10-min intervals, from 1 May 2015 to 30 September 2017.

Plant population characteristics

L. chinensis is a typical rhizomatous grass, and *S. grandis* and *S. krylovii* are bunch grasses. The aboveground biomass of *S. grandis* and *L. chinensis* was 63.4–73.5% of the total aboveground biomass in the *S. grandis* grassland and that of *S. krylovii* and *L. chinensis* was 77.4–95.2% in the *S. krylovii* grassland. In the *S. grandis* grassland, we monitored plant phenology, population characteristics, and root biomass of *S. grandis* and *L. chinensis*. In the *S. krylovii* grassland, we monitored *S. krylovii* and *L. chinensis*.

Leaf-out day, first flowering day, and first withering day indicated the returning green, reproductive, and withering stages, respectively, which were the main stages of plant growth. A total of fifteen individual plants of each species (five individuals per block × three blocks) were randomly selected in each treatment of both grasslands and labeled before each growing season. Plant phenology was monitored every 3–5 d from 15 April to 15 October over the growing season of 2015–2017 (Ji et al. 2017). During phenological changes, the frequency of observation increased to every two days. The leaf-out day was the day that the first leaf was observed for each marked individual (Ji et al. 2017). The first

flowering day and the first withering day were also recorded.

Nine 1 × 1 m quadrats (three quadrats per block × three blocks) were randomly set in each treatment of both grasslands on 1 August 2015–2017. For each quadrat, the cover (%), plant height (cm), and density (individual per m^2) of each species were recorded. In this study, the density of *L. chinensis* was counted by individual and the density of *S. grandis* and *S. krylovii* by clumps. To determine aboveground biomass (g), the aboveground parts of each individual were clipped near the soil surface and dried at 65°C for 48 h to a constant weight.

According to Chen et al. (2001)'s study, the root biomass of *S. grandis* concentrated in the soil depth of 0–30 cm and that of *S. krylovii* and *L. chinensis* in 0–25 cm and 0–20 cm, respectively (Chen et al. 2001). In each treatment of both grasslands, nine individual plants of each species (three individuals per block × three blocks) were randomly selected and dug up on 1 August 2015 and 2016 (the weather was too dry in 2017), removing all the soil and roots in a radius of 30 cm and depth of 50 cm. According to root morphological characteristics of the three species (Appendix S1: Fig. S1), roots were washed from topsoil to deep soil carefully to remove soil, separated, and placed into envelopes and then dried at 65°C for 48 h to a constant weight.

Data analyses

Soil temperature in the daytime and nighttime was indicated by the mean soil temperature between 6:00 am–6:00 pm and 6:00 pm–6:00 am (local time), respectively (Xia et al. 2010). The effects of litter accumulation on soil temperature were indicated by the soil temperature difference between the control treatment and the litter removal treatment, calculated by the following equation (Hou et al. 2019):

$$\text{Soil temperature difference} = ST_C - ST_E,$$

where ST_C is the mean soil temperature in the control treatment and ST_E is the mean soil temperature in the litter removal treatment. To examine differences in the mean soil temperature in the daytime and nighttime among different months and during the growing season, we used repeated-measures ANOVA.

To test for the effect of litter accumulation on plant phenology, the phenological date was first transformed into the Julian day. Then, we compared the mean leaf-out day, first flowering day, and first withering day of each species using a general linear model with treatment and block as factors. In this study, block had no significant effect on the plant phenology ($P > 0.05$).

Population-level characteristics of the three species were indicated by the means of plant height, cover, and density in the nine quadrats of each treatment. Root characteristics were indicated by the mean of root biomass of the nine individuals in each treatment of both grasslands. The relative dominance of the three species was indicated by the mean relative aboveground biomass in the nine quadrats of each treatment. It was calculated by the following equation:

$$\text{Relative dominance} = B_i/B,$$

where B_i is aboveground biomass of a species and B is the total aboveground biomass in this quadrat.

To test for the effect of litter accumulation on cover, plant height, density, root biomass, and relative dominance of the three species, we used a general linear model with treatment and block as factors. In this study, block had no significant effect on the population characteristics ($P > 0.05$). All statistical analyses were conducted in SPSS 21.0 (IBM, Chicago, Illinois, USA).

Results

Asymmetric effects of litter accumulation on soil temperature

Compared with the litter removal treatment, litter accumulation significantly decreased soil temperature in the control plots of both grasslands, with a larger effect in the daytime than in the nighttime (Fig. 1; Appendix S1: Fig. S2; $P < 0.05$). This negative effect was greater at 2.5 cm depth than 12.5 cm (Fig. 1; Appendix S1: Fig. S2; $P < 0.0001$). For example, in the *S. grandis* grassland, litter accumulation decreased soil temperature at 2.5 cm depth in the daytime by 2.3°–6.3°C and in the nighttime by 0.0°–0.8°C. The decrease was much lower at 12.5 cm depth (1.6°–2.2°C in the daytime and 1.4°–3.1°C in the nighttime; Appendix S1: Fig. S2). In the *S.*

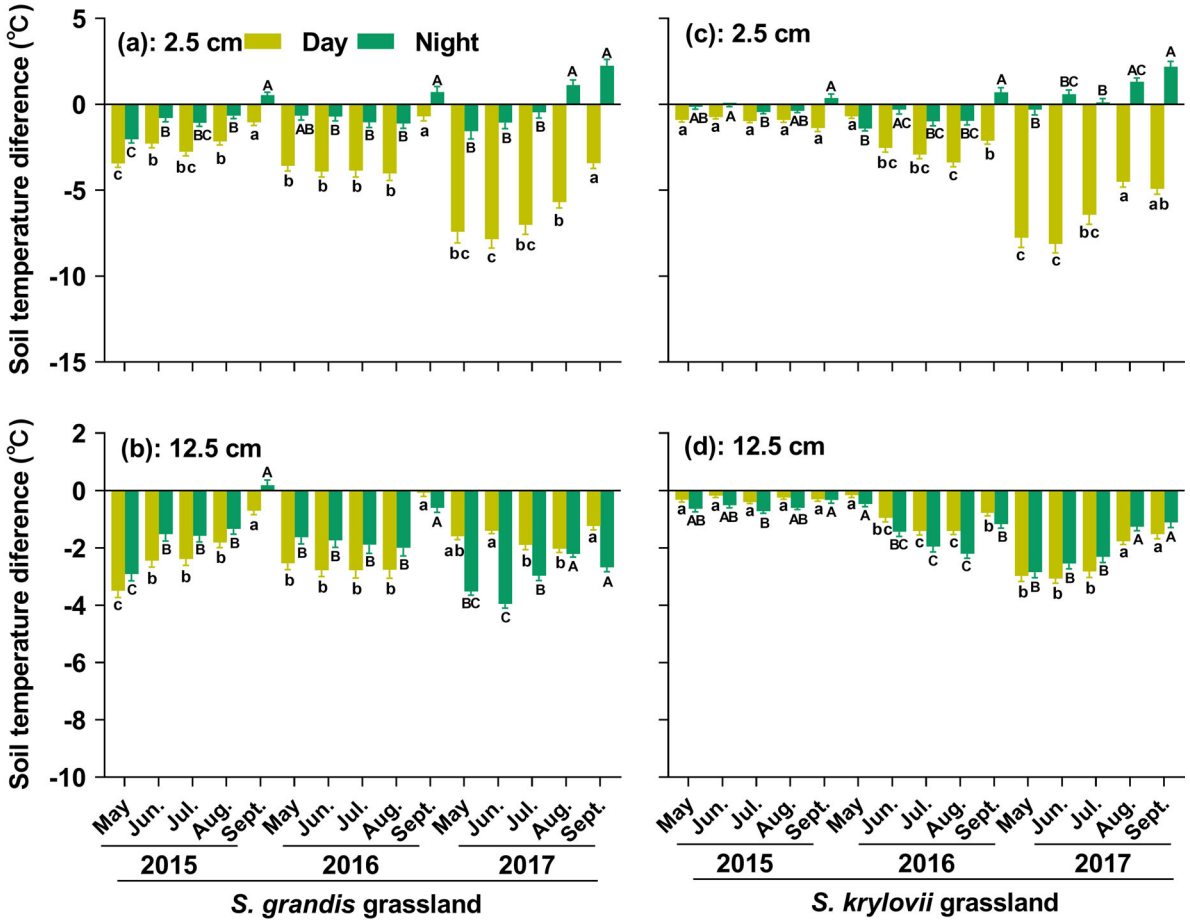


Fig. 1. Monthly dynamics of soil temperature difference in the daytime and nighttime between the two treatments. Data were mean + 1 SE; different lowercase and uppercase letters, respectively, indicated that there were significant differences among the monthly soil temperature difference in the daytime and nighttime at 0.05 level.

krylovii grassland, litter accumulation decreased soil temperature at 2.5 cm depth in the daytime by 1.0°–6.3°C and in the nighttime by −0.8°–0.6°C. Again, the decrease was less at 12.5 cm depth (0.3°–2.4°C in the daytime and 0.6°–2.0°C in the nighttime; Appendix S1: Fig. S2). The negative effect of litter accumulation on soil temperature gradually weakened during the growing season (Fig. 1; $P < 0.05$), and in the late growing season even shifted to a positive effect during the nighttime (Fig. 1; $P < 0.05$).

Asymmetric effects of litter accumulation on plant phenology

Litter accumulation in the control plots delayed the leaf-out day, first flowering day, and first withering day of the three species of both grasslands compared with the removal treatment (Fig. 2; $P < 0.05$). The delay in *S. grandis* or *S. krylovii* was significantly longer than *L. chinensis* in the control plots of both grasslands, respectively (Fig. 2; *t*-test: $P < 0.05$). For example, the leaf-out days of *S. grandis* and *S. krylovii* were postponed by 16.9–24.3 d and 9.3–11.7 d (Fig. 2a and c), but that of *L. chinensis* was only postponed by 5.1–6.7 days in the *S. grandis* grassland and 2.1–3.2 d in the *S. krylovii* grassland (Fig. 2b and d).

Furthermore, the earlier phenological stages were more delayed than the later ones (Fig. 2). For instance, in the control of the *S. grandis* grassland, the delay of leaf-out (in the early growing

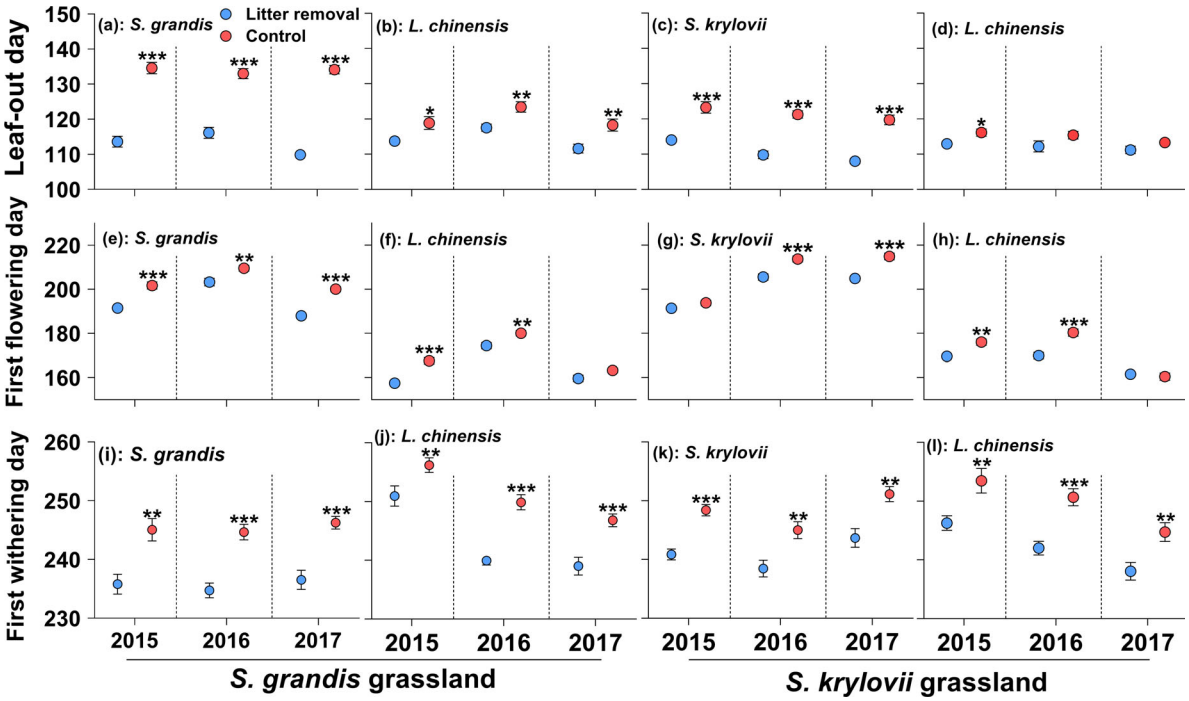


Fig. 2. Plant phenology of the three species between the two treatments. (a–d) indicated leaf-out day of the three species; (e–h) indicated first flowering day of the three species; (i–l) indicated first withering day of the three species; time series were used the Julian day; data were mean + 1 SE and$N = 15$; and *, **, and *** indicated that there were significant differences in leaf-out day, first flowering day, and first withering day of the three species between the two treatments at 0.05, 0.01, and 0.0001 levels, respectively.

season) in *S. grandis* was 16.9–24.3 d and in *L. chinensis* was 5.1–6.7 d (Fig. 2a and c), whereas the first withering day in *S. grandis* (delayed 9.3–9.7 d) was similar to that in *L. chinensis* (5.3–9.9 d) in the late growing season (Fig. 2i–l).

Asymmetric effects of litter accumulation on population characteristics

Litter accumulation had no significant effect on the plant height of *S. grandis* or *S. krylovii* (Fig. 3a and c), but significantly increased the height of *L. chinensis* by 66.7–77.5% in the *S. grandis* grassland and 30.2–54.2% in the *S. krylovii* grassland (Fig. 3b and d; $P < 0.05$). Litter accumulation reduced the cover of *S. grandis* or *S. krylovii* in the control plots of both grasslands (Fig. 3e and g; $P < 0.01$). In contrast, the cover of *L. chinensis* increased in the control plots of both grasslands (Fig. 3f and h; $P < 0.05$). Litter accumulation decreased the density of *S. grandis* and *S. krylovii* (Fig. 3i and k; $P < 0.05$), but had no significant effect on *L. chinensis* (Fig. 3j and l).

In 2015, litter accumulation had no significant effects on the root biomass of *S. grandis* or *S. krylovii* (Fig. 4a and c), but in 2016 the root biomass was significantly greater in the litter removal treatments of both grasslands (Fig. 4a and c; $P < 0.05$). The root biomass of *L. chinensis* reduced in the litter removal treatments of both grasslands in 2015 and 2016 ($P = 0.059$ and 0.051; Fig. 4b and d).

Litter accumulation altered the relative dominance of the three species in both grasslands (Fig. 5). The relative dominance of *S. grandis* or *S. krylovii* was significantly lower in the control plots of both grasslands (Fig. 5a and c; $P < 0.01$), but the relative dominance of *L. chinensis* was greater (Fig. 5b and d; $P < 0.01$).

Discussion

Litter accumulation asymmetrically altered soil temperature, plant phenology, and population characteristics of three dominant species in

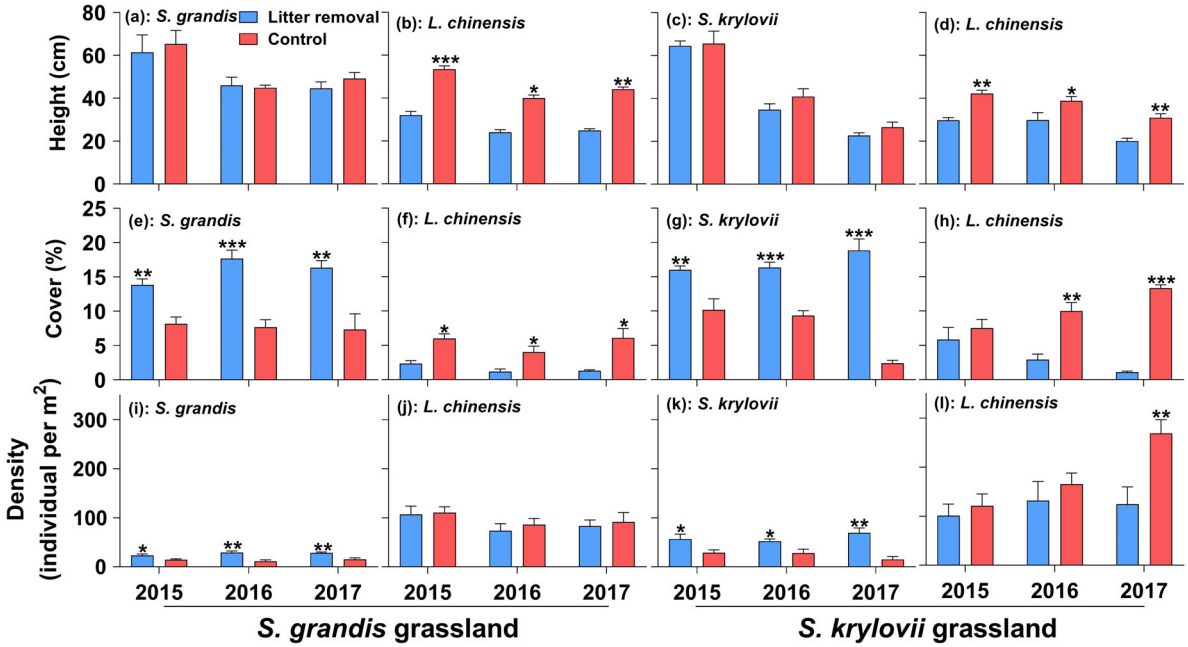


Fig. 3. Population characteristics of the three species between the two treatments. (a–d) indicated the plant height of the three species; (e–h) was the cover of the three species; (i–l) was the density of the three species; data were mean + 1 SE and$N = 9$; and *, **, and *** indicated that there were significant differences in plant height, cover, and density between the two treatments at 0.05, 0.01, and 0.0001 levels, respectively.

fenced grasslands in Inner Mongolia, China. Litter accumulation decreased soil temperatures, more so in the daytime than the nighttime, except late in the growing season when litter accumulation increased nighttime soil temperatures. The decreased soil temperature delayed plant phenology, longer in *S. grandis* or *S. krylovii* than *L. chinensis*. These abiotic and phenological changes asymmetrically altered population characteristics of the three species, thereby changing population dynamics.

Effects of litter accumulation on soil temperature

Litter accumulation decreased soil temperature in the control plots of both experimental grasslands, consistent with many previous studies (Facelli and Pickett 1991, Weltzin et al. 2005). More importantly, we found that this negative effect was greater in the daytime than in the nighttime, particularly at shallow (2.5 cm) depths (Fig. 1; Appendix S1: Fig. S2). This result indicated that litter accumulation has complicated and asymmetric effects on soil temperature depending on the time of day, with the transfer of thermal energy from air to the soil during the day reversing during the night (Xia et al. 2010). The shading effect of litter reduces the daytime heat absorption of soil, but the physical barrier of litter creates a warming effect to inhibit heat loss from soil during the night (Facelli and Pickett 1991). Overall, the shading effect of litter accumulation was greater than the warming effect. In addition, it also shows that litter accumulation decreased soil temperature, owing to the decrease in soil temperature in the daytime. Compared with the warming effect, the shading effect of litter accumulation had a dominant effect on soil temperature in fenced grasslands. Thus, the strong temporal variation in these shading and warming effects of litter must be accounted for in future studies.

Over longer time scales, such as a growing season, the negative effect of litter accumulation on daytime soil temperatures gradually weakened, but the negative effect in the nighttime shifted to a positive effect by in the late growing season (Fig. 1). This result indicated that litter accumulation has different effects on soil temperature in

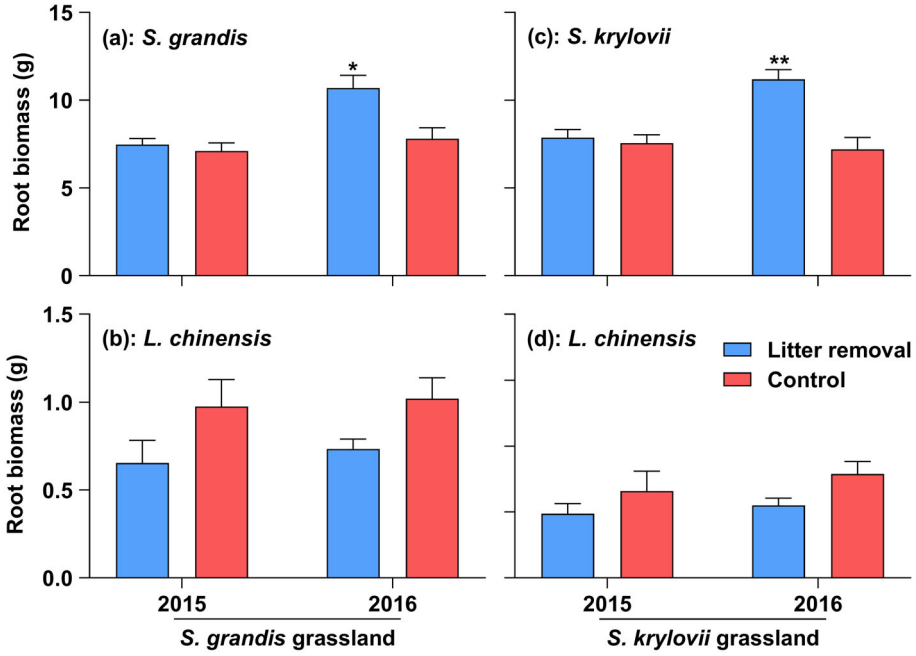


Fig. 4. Root biomass of the three species between the two treatments. Data were mean + 1 SE and$N$ = 9; and * and ** indicated that there were significant differences in root biomass between the two treatments at 0.05 and 0.01 levels, respectively.

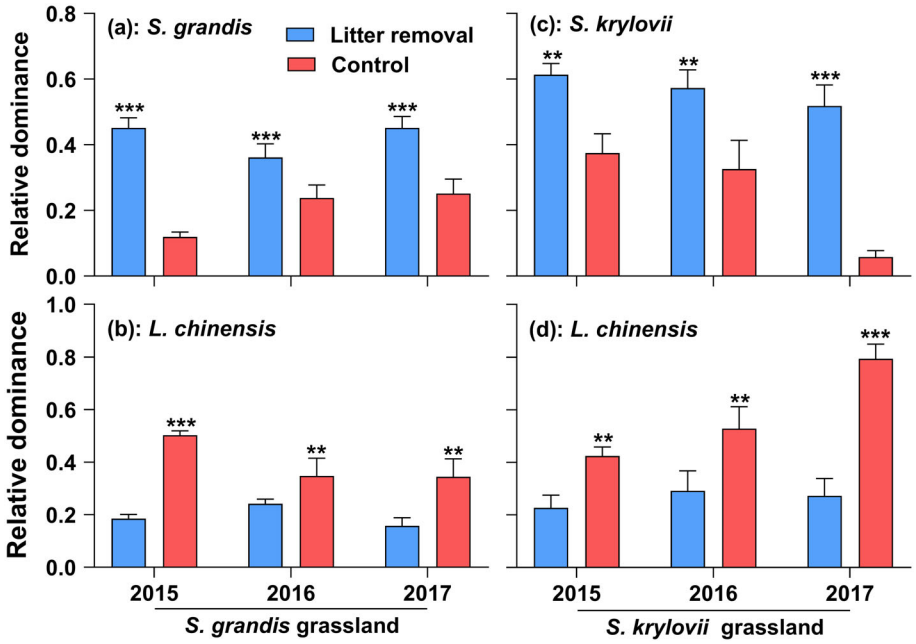


Fig. 5. Relative dominance of the three species between the two treatments. Data were mean + 1 SE and$N$ = 9; and ** and *** indicated that there were significant differences in relative dominance of the three species between the two treatments at 0.01 and 0.0001 levels.

the day versus the night at different stages of the growing season. In the early growing season, litter accumulation severely postponed increase in soil temperature through reducing the heat absorption of soil, whereas had a weak warming effect on soil temperature in the nighttime because of lower soil temperature. Therefore, litter accumulation had a negative effect on soil temperature in the early growing season, supporting some previous studies (Facelli and Pickett 1991). Over the growing season, soil temperature gradually increased in both grasslands with the increase in solar radiation over the year. In contrast, the shading effect of litter gradually reduced across time due to the increase in plant growth. Increasing insolation and plant growth might therefore decrease the effectiveness of litter shading on soil temperature over the growing season. However, the accumulation of litter later in the growing season decreases the heat exchange between soil and air in the nighttime, resulting in a positive effect on soil temperature, consistent with previous studies (Facelli and Pickett 1991).

Soil temperature is a critical ecological factor that affects plant growth and regulates biological processes in terrestrial ecosystems (Field et al. 1992). Slight changes in soil temperature can alter soil moisture, soil respiration rate, and nutrient cycling (Xia et al. 2010). These soil processes might well be altered by the effect of litter accumulation on soil temperatures in fenced grasslands, probably more in the daytime (e.g., Fig. 1). These soil processes were not measured in this study but should be considered in future research.

Soil temperature was strongly coupled with soil moisture, such that litter accumulation could indirectly increase soil moisture in fenced grasslands (Appendix S1: Fig. S3) by decreasing soil temperature (Deutsch et al. 2010, Xia et al. 2010). Moreover, a decrease in soil temperature could delay thawing of soil in the early growing season (Facelli and Pickett 1991). But an increase in soil temperature and moisture later in the year could extend the growing season and postpone soil freezing (Watt 1970, Facelli and Pickett 1991). For plant communities, lower soil temperatures could inhibit seed germination, delay plant phenology (Fig. 2), and reduce growth rates, all of which may affect the life history, phenology, and function of affected plants.

Effect of litter accumulation on plant phenology

Plant phenology is an indicator of plant growth that is sensitive to environmental changes such as air temperature, precipitation, and soil temperature and moisture (Cleland et al. 2007, Shen et al. 2018). Soil temperature is an important driver of plant phenology (Ji et al. 2017), an increase in which can advance leaf unfolding but delay leaf coloring in many regions (Peñuelas and Filella 2001). Similarly, an increase in soil moisture can advance plant phenology (Zhu et al. 2016). In this study, litter accumulation significantly delayed leaf-out, first flowering, and first withering of the three species in control plots of both grasslands (Fig. 2). The delay in leaf-out may have postponed first flowering and first withering. Alternatively, increased soil temperature and moisture (Fig. 1; Appendix S1: Figs S2 and S3) may have extended the growing season (Liu et al. 2016). Differences in plant phenology between the species may have been driven by root morphology. Leaf-out was delayed more in the deeper-rooted *S. grandis* and *S. krylovii* than in the shallower-rooted *L. chinensis* (Fig. 2), maybe because of a greater availability of soil moisture to *L. chinensis*. In addition, denser litter appeared to have more negative effects on leaf-out of *S. grandis* and *S. krylovii* (Hou, *personal observation*).

Interestingly, our results were opposite to some previous studies. For example, Zhu et al. (2016) reported that plant phenology was significantly advanced in a fenced alpine meadow in Tibet, likely due to soil moisture rather than soil temperature. However, compared with the dominant species in the alpine meadow (e.g., *Kobresia pygmaea* and *Potentilla saundersiana*), *L. chinensis*, *S. grandis,* and *S. krylovii* have relatively deeper roots that are less sensitive to increases in shallow soil moisture. Additionally, the arid and semiarid grasslands in Inner Mongolia have lower water requirements and sensitivity than the Tibetan alpine meadow. Moreover, Zhu et al. (2016) stressed the reproductive stage of *K. pygmaea* was delayed after five years fencing. It indicated that fencing time might be another critical factor to regulate plant phenology. Our fencing time was longer than the previous study. Thus,

the effects of fencing and litter accumulation on plant phenology may vary depending on habitat and time since fencing, as well as plant habit, life form, and other traits.

Effects of litter accumulation on population characteristics

Species showed different sensitivities to litter accumulation in characteristics such as plant height, cover, and biomass. In this study, litter accumulation increased the height, cover, and root biomass of *L. chinensis*, but decreased cover, density, and root biomass of *S. grandis* and *S. krylovii* in the control plots of both grasslands (Fig. 3), indicating that *L. chinensis* has a higher tolerance to litter accumulation than *S. grandis* and *S. krylovii*. During the experiment, the abiotic environment of the control plots became shaded and moister, because of reduced light (Jensen and Gutekunst 2003, Hou et al. 2019), lower soil temperature (Fig. 1; Appendix S1: Fig. S2), and higher soil moisture (Appendix S1: Fig. S3). Plants may grow taller as they compete for light in more shaded environments, aided by more soil moisture (Wang et al. 2011). The shallower roots of *L. chinensis* may have allowed it to take advantage of the greater soil moisture (Bai et al. 2009); this species also tends to be better adapted to the moister environments (Chen et al. 2005, Wang et al. 2011) created by litter accumulation. It seems likely that litter accumulation alters asymmetric resource acquisition patterns of different species that then alters the original interspecific competitive relationships.

Fencing and subsequent litter accumulation changed the relative dominance of *S. grandis* or *S. krylovii* to *L. chinensis* in terms of aboveground biomass (Fig. 5). This phenomenon, where litter accumulation changes community composition and structure, has been reported in many fenced herbaceous plant communities, including in the Inner Mongolia (Hou et al. 2019), the Loess Plateau (Jing et al. 2013), the Mediterranean (Golodets et al. 2010), America (Weltzin et al. 2005), and England (Medina-Roldan et al. 2012). Litter accumulation has these effects through changes to the abiotic environment (such as light and soil temperature and moisture, detailed above), as well as direct effects on recruitment and growth through the physical barrier to seed dispersal and germination (Jensen and Gutekunst 2003, Loydi et al. 2013). These effects on the population dynamics of species ultimately determine species richness and community evenness, composition, and structure, and are likely to drive community successional change in fenced communities (Hou et al. 2019). These findings emphasize the direct role of litter accumulation in plant population and community dynamics and suggest that litter should be taken into account in the management of grasslands.

Implications of litter on grassland management

Litter is regarded as one indicator of the health of grassland ecosystems (Wang et al. 2011). We have shown that fencing accelerates litter accumulation that then alters the abiotic environment, plant phenology, and plant population characteristics (Figs. 1–4), often in complex ways. In grassland management, the function of litter should be fully considered and it may be better to avoid excess litter accumulation. Additionally, although the grassland ecosystem service and function were improved (indicated by the increase in plant height, cover, and aboveground biomass of plants), nutrition and quality of forage grass may be reduced due to the mixture and decay of litter. Long-term fencing may also result in a decrease in the use efficiency of grassland resources. Therefore, grasslands should be appropriately used when enclosed to avoid any negative effects of long-term fencing.

Conclusions

Many grasslands in northern China have suffered from severe degradation in the last few decades. Fencing was regarded as a useful method for restoring degraded grasslands, due to the low investment and quick response of grasses. However, excess litter accumulates on the soil surface, generally decreasing soil temperature, although these effects vary over daily cycles and the growing season. These changes in the abiotic environment delayed leaf-out, flowering, and wilting of *S. grandis*, *S. krylovii,* and *L. chinensis*, with bigger effects on the deeper-rooted *S. grandis* and *S. krylovii*, as well as on the performance and relative abundance dominance of all grasses. Changes to the successional dynamics mean that *S. grandis* and *S. krylovii* could potentially even be replaced by *L. chinensis*

in both fenced grasslands, respectively. Our findings elucidate the mechanisms of interaction between the abiotic environment and plant community after litter accumulation and suggest that litter should be fully considered in grassland management. Degraded grasslands should be appropriately managed during enclosure to avoid having to maintain fencing over the long term.

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Literature Cited

Amatangelo, K. L., J. S. Dukes, and C. B. Field. 2008. Responses of a California annual grassland to litter manipulation. Journal of Vegetation Science 19: 605–612.

Bai, W. M., X. Q. Sun, Z. W. Wang, and L. H. Li. 2009. Nitrogen addition and rhizome severing modify clonal growth and reproductive modes of *Leymus chinensis* population. Plant Ecology 205:13–21.

Chen, S. P., Y. F. Bai, L. X. Zhang, and X. G. Han. 2005. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. Environmental and Experimental Botany 53:65–75.

Chen, S. H., H. Zhang, L. Q. Wang, B. L. Zhan, and M. L. Zhao. 2001. Root system of grassland plants in north China. Jilin University Press, Changchun, China.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22:357–365.

Deutsch, E. S., E. W. Bork, and W. D. Willms. 2010. Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. Agriculture, Ecosystems & Environment 135:1–9.

Eckstein, R. L., and T. W. Donath. 2005. Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. Journal of Ecology 93:807–816.

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. The Botanical Review 57:1–32.

Field, C. B., F. S. Chapin, P. A. Matson, and H. A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. Annual Review of Ecology and Systematics 23:201–235.

Golodets, C., J. Kigel, and M. Sternberg. 2010. Recovery of plant species composition and ecosystem function after cessation of grazing in a Mediterranean grassland. Plant and Soil 329:365–378.

Han, X. G., K. Owens, X. B. Wu, J. G. Wu, and J. H. Huang. 2009. The grasslands of Inner Mongolia: a special feature. Rangeland Ecology & Management 62:303–304.

Hou, D. J., W. M. He, C. C. Liu, X. G. Qiao, and K. Guo. 2019. Litter accumulation alters the abiotic environment and drives community successional changes in two fenced grasslands in Inner Mongolia. Ecology and Evolution 9:9214–9224.

Hovstad, K. A., and M. Ohlson. 2008. Physical and chemical effects of litter on plant establishment in semi-natural grasslands. Plant Ecology 196:251–260.

Jensen, K., and K. Gutekunst. 2003. Effects of litter on establishment of grassland plant species: the role of seed size and successional status. Basic and Applied Ecology 4:579–587.

Ji, S. N., A. T. Classen, Z. H. Zhang, and J. S. He. 2017. Asymmetric winter warming advanced plant phenology to a greater extent than symmetric warming in an alpine meadow. Functional Ecology 31:2147–2156.

Jing, Z. B., J. M. Cheng, and A. Chen. 2013. Assessment of vegetative ecological characteristics and the succession process during three decades of grazing exclusion in a continental steppe grassland. Ecological Engineering 57:162–169.

Kang, L., X. G. Han, Z. B. Zhang, and J. X. Sun. 2007. Grassland ecosystems in China: review of current knowledge and research advancement. Philosophical Transactions of the Royal Society B: Biological Sciences 362:997–1008.

Kelemen, A., P. Török, O. Valkó, T. Miglécz, and B. Tóthmérész. 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.

Letts, B., E. G. Lamb, J. M. Mischkolz, and J. T. Romo. 2015. Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. Plant Ecology 216:357–370.

Liu, J. K., Z. Bian, K. B. Zhang, B. Ahmad, and A. Khan. 2019. Effects of different fencing regimes on community structure of degraded desert grasslands on Mu US desert, China. Ecology and Evolution 9:3367–3377.

Liu, J. H., J. J. Wu, H. B. Su, Z. H. Gao, and Z. T. Wu. 2017. Effects of grazing exclusion in Xilin Gol grassland differ between regions. Ecological Engineering 99:271–281.

Liu, Q., Y. S. Fu, Z. Z. Zeng, M. T. Huang, X. R. Li, and S. L. Piao. 2016. Temperature, precipitation, and insolation effects on autumn vegetation phenology in temperate China. Global Change Biology 22: 644–655.

Liu, Y. S., X. H. Yang, D. S. Tian, R. C. Cong, X. Zhang, Q. M. Pan, and Z. J. Shi. 2018. Resource reallocation of two grass species during regrowth after defoliation. Frontiers in Plant Science 9:1–11.

Loydi, A., R. L. Eckstein, A. Otte, and T. W. Donath. 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. Journal of Ecology 101:454–464.

Medina-Roldan, E., J. Paz-Ferreiro, and R. D. Bardgett. 2012. Grazing exclusion affects soil and plant communities, but has no impact on soil carbon storage in an upland grassland. Agriculture Ecosystems & Environment 149:118–123.

Peñuelas, J., and I. Filella. 2001. Phenology-Responses to a warming world. Science 294:793–795.

Ruprecht, E., T. W. Donath, A. Otte, and R. L. Eckstein. 2008. Chemical effects of a dominant grass on seed germination of four familial pairs of dry grassland species. Seed Science Research 18:239–248.

Sagar, R., G. Y. Li, J. S. Singh, and S. Q. Wan. 2019. Carbon fluxes and species diversity in grazed and fenced typical steppe grassland of Inner Mongolia, China. Journal of Plant Ecology 12:10–22.

Shen, X. J., B. H. Liu, M. Henderson, L. Wang, Z. F. Wu, H. T. Wu, M. Jiang, and X. G. Lu. 2018. Asymmetric effects of daytime and nighttime warming on spring phenology in the temperate grasslands of China. Agricultural and Forest Meteorology 259:240–249.

Song, Y. T., L. L. Li, Q. Li, W. Y. Na, and D. W. Zhou. 2018. Plant litter effects inversely on air and soil temperatures in *Leymus chinensis* grassland, Northeast China. IOP Conference Series: Earth and Environmental Science. https://doi.org/10.1088/1755-1315/146/1/012005

Wang, J., M. L. Zhao, W. D. Willms, G. D. Han, Z. W. Wang, and Y. F. Bai. 2011. Can plant litter affect net primary production of a typical steppe in Inner Mongolia? Journal of Vegetation Science 22:367–376.

Watt, A. S. 1970. Contributions to ecology of Bracken (*Pteridium aquilinum*). 7. Bracken and litter. 3. cycle of change. New Phytologist 69:431–449.

Weltzin, J. F., J. K. Keller, S. D. Bridgham, J. Pastor, P. B. Allen, and J. Chen. 2005. Litter controls plant community composition in a northern fen. Oikos 110:537–546.

Wiesmeier, M., M. Steffens, A. Kölbl, and I. Kögel-Knabner. 2009. Degradation and small-scale spatial homogenization of topsoils in intensively-grazed steppes of Northern China. Soil & Tillage Research 104:299–310.

Willms, W. D., S. M. McGinn, and J. F. Dormaar. 1993. Influence of litter on herbage production in the mixed prairie. Journal of Range Management 46:320–324.

Xia, J. Y., S. P. Chen, and S. Q. Wan. 2010. Impacts of day versus night warming on soil microclimate: results from a semiarid temperate steppe. Science of the Total Environment 408:2807–2816.

Xiong, S. J., and C. Nilsson. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 87:984–994.

Zhu, J. T., Y. J. Zhang, and Y. J. Liu. 2016. Effects of short-term grazing exclusion on plant phenology and reproductive succession in a Tibetan alpine meadow. Scientific Reports 6:27781.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3289/full