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The fertile island effect collapses under extreme overgrazing: evidence from a shrub-encroached grassland

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Abstract
Background and aims Woody plant encroachment is a phenomenon of global concern in drylands due to demonstrated reductions in livestock carrying capacity. However, shrubs are known to contribute to the development of patches of enhanced fertility that might offset any negative effects of increasing grazing. We measured soil physical and chemical characteristics within shrub and open patches across a gradient in livestock grazing to explore how the relative effect of shrubs might change with increasing grazing-induced disturbance.
Methods Soil carbon, nitrogen phosphorus and bulk density were measured within 92 shrub patches and their paired interspaces at five sites ranging from long-grazed to long-ungrazed in a semiarid grassland encroached by the N-fixing shrub *Caragana microphylla*. We used a combination of linear and structural equation modelling to test whether shrubs might buffer any negative effects of overgrazing on soils.
Results Shrub soils were more porous, and had more organic carbon, nitrogen and phosphorus than interspace soils. Within both microsites, however, soil bulk density increased, and soil organic carbon and nutrients declined, with increasing grazing intensity. Grazing reduced interspace plant cover and height and exacerbated the negative effects of bulk density on soil carbon, whereas shrubs had the opposite effect. The relative importance of shrubs for soil carbon and nutrients increased with increasing grazing intensity but collapsed under extreme overgrazing.
Conclusions These findings highlight the effect of grazing in promoting shrub dominance, which can also prevent grassland degradation. However, any positive effects of grazing collapsed when sites were severely overgrazed.

Keywords Fertile patch · Overgrazing · Shrub · Soil nutrients · Temperate grassland

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Introduction

A distinctive feature of dryland ecosystems is the concentration of resources (nutrients, organic matter, seeds, water) beneath perennial patches at the expense of the less fertile interspaces (García-Moya and McKell 1970). These resource-rich 'fertility islands' are maintained by processes of wind and water erosion, and complex interactions among individual plants and the surrounding soil matrix (Garner and Steinberger 1989; Seghieri and Galle 1999). The formation of fertile islands centered on woody plant canopies is a dynamic process that involves several key ecological processes. Woody plants moderate fluctuations in radiation and surface temperature (Yan et al. 2018), and enhance the distribution of plant-induced macropores that are critical for conducting water (Colloff et al. 2010). Deep-rooted woody plants can extract nutrients from deep in the subsoil, and scavenge resources from the interspaces to support a greater biomass of above-ground material; the decomposition of which releasing nutrients into the soil beneath the plants, reinforcing their fertility (Gherardi et al. 2013; Lynch and Whipps 1990). In addition, greater canopy size and plant growth beneath woody canopies increases threshold wind velocities, so that atmospheric dust and windblown sediments derived from the interspaces are deposited around the plants, further reinforcing the fertile island effect (Reynolds et al. 1999; Yan et al. 2019; Zhang et al. 2011). Finally, these processes result in woody canopies becoming preferred sites for plants and animals, including microorganisms, whose detritus enhances soil carbon (C) and nitrogen (N), further enriching understorey soils (Aguilera et al. 1999; Dean et al. 1999).

While much has been written about the impacts on woody plants on plant and soil function, and the processes that drive their formation (e.g. biological and abiotic processes), relatively little is known about changes in the fertile island effect associated with woody plant patches subjected to different levels of human-induced disturbance, such as those associated with overgrazing by livestock. Fertile island persistence has been shown to be as little as a few months for grasses (Kelly and Burke 1997), to a few years for shrubs such as *Artemisia tridentate* (Bechtold and Inouye 2007) or many years account for some trees (Eldridge and Wong 2005). Thus, we would expect the relative fertile island effect to intensify with increasing plant size, given greater investment by plants in the maintenance of their soil environment. More recently, Allington and Valone (2014) showed that the fertile island effect was more pronounced in the presence of grazing, and that grazing might be responsible for the occurrence of the fertile island effect in shrublands. The effects of different levels of grazing on the relative fertile island effect, however, have been little studied, which is surprising, given the extent of grazing worldwide and its pervasive effects on many ecosystems (Fleischner 1994). Understanding any interactive effects of shrub patch formation and changes in land use intensification is critically important to allow us to better manage grasslands and shrublands to support pastoral production and ecosystem services and therefore human well-being.

Grazing by livestock occupies about a quarter of the global terrestrial land mass, most of it in drylands, and worldwide, supports millions of people and their cultures (Asner et al. 2004). Unmanaged grazing, however, can lead to substantial negative effects on ecosystem structure and function (Fleischner 1994), by reducing plant vigour, shifting the composition from perennial plants to annuals, often leading to erosion and depletion of organic matter and nutrients such as nitrogen and phosphorus (Vaieretti et al. 2018; Yan et al. 2013). In China's Inner Mongolian grasslands, for example, overgrazing has resulted in substantial reductions in grassland productivity and in some areas is associated with the encroachment of thorny, unpalatable shrubs such as *Caragana microphylla* (Yan et al. 2019). Encroachment presents considerable challenges to land managers, pastoralists and government. Encroachment also alters the distribution of resources between interspaces and shrub hummocks (Schlesinger and Pilmanis 1998), and has been shown to lead to the reinforcement of the fertile island effect (Allington and Valone 2014). Sites with widely different intensities of grazing in Inner Mongolian encroached grasslands provided us with a unique opportunity to examine the nature of the relationship between increasing grazing intensity and the relative fertile island effect. We hypothesized that continuous overgrazing will substantially reduce vegetation quality and soil function. Thus, the fertile island effect due to shrubs should intensify under grazing as plant and soil condition in the interspaces declines more than that beneath the shrubs. This would happen via a strengthening of the process of resource redistribution from the interspaces to the shrubs. However, continued heavy overgrazing would eventually lead to a collapse of the fertile island effect when the actual shrubs are destroyed under the action of grazing, thereby compromising their capacity to trap eroded material.

We tested these hypotheses in a shrub-encroached grassland across a wide gradient in grazing intensity.

We sampled soil C, nutrients, and bulk density beneath shrubs and in their paired interspaces, at five large sites that representing a gradient in increasing grazing intensity from long-ungrazed to historically extremely overgrazed, to test the relative fertile island effect on C, nutrients and soil density.

Methods

Site description

The study was conducted in typical grasslands at an altitude of about 1200 m above sea level in the region of the Xilin River in Inner Mongolia, China (43.7°N, 116.07°E). The climate is semiarid, with an annual average rainfall of 298 mm (1981–2016). Precipitation is highly variable, with 75% occurring from June to September. Mean annual evaporation is 1600–1800 mm. Strong winds occur from March to May with an average monthly speed of up to 4.9 m s^{-1}. The average temperature is −23.3 °C in the coldest month (January) and 20.4 °C in the hottest month (July), with a frost-free period of about 100 days. The soils are typically chestnut and calcic chernozems with sandy surface texture resulting from substantial wind erosion (Yan et al. 2011). The dominant native plant species found in the steppe are *Stipa grandis* P., *Cleistogenes squarrosa* Trin., *Artemisia frigida* Willd., and *Leymus chinensis* Trin. (Yan et al. 2019). Due to variable levels of overgrazing, the grassland vegetation shows evidence of severe degradation, and some sites are heavily encroached by the shrub *Caragana microphylla* with shrub cover varying from <5% to about 30% (Yan et al. 2016, 2019).

Experimental design

The experiment was conducted in mid-August 2018 at five large (> 6 ha) sites (paddocks) that represented a gradient in livestock grazing from long ungrazed to extremely overgrazed. The five sites were characterized as the following: 1) long ungrazed (LU) site that has been ungrazed for the past 35 years (16 ha), 2) moderately ungrazed (MU) with 19 years of exclosure (24 ha), 3) a site that was recently ungrazed (RU) 2 years prior to our study (6 ha), 4) moderately overgrazed (MO) site with stocking rates of 2–3 sheep units ha^{-1} (80 ha), and 5) extremely overgrazed (EO) site with >3 sheep units ha^{-1} (20 ha). The categorical grazing levels were identified by obtaining information from local herdsman. All sites had similar topography and slope (< 1%) and were separated by distances of <6 km.

Strictly speaking, our study was pseudoreplicated, given that there was only one replicate site of each of the five levels of grazing. However, we stress the following. First, our units of interest, the individual shrubs, shrub mounds and adjacent interspaces were spatially independent sub-samples in a statistical sense because they were widely spaced and the sites were relatively large. Second, measurements of plant and soil attributes provide additional evidence that this gradient represents a true grazing-induced degradation gradient. For example, *Artemisia frigida* and *Cleistogenes squarrosa* dominate sites that with high levels of overgrazing (Liu et al. 2002). Significant differences in plant and soil properties among the five sites (Table S1) reflect clear differences in grazing management among the five sites. Despite the pseudoreplication at the scale of grazing intensity, our results can provide important insights into soil and plant processes operating in shrublands. We recognize, however, that our study conclusions can only be directly applied to the immediate environment in which our study was carried out.

Shrub size, mound height and plant biomass

To examine the relationship between grazing and the fertile island effect, we randomly selected 16 to 20 shrubs of various size from about 2 to 10 m^2 (92 shrubs in total across the five sites). To minimize potential interactions among individual shrubs, we selected shrubs >20 m apart. We then measured shrub size (two diameters through the shrub centre), shrub height and plant cover. Shrub height was measured from the base of the stem to the top of the tallest live branch. Heights of the 92 shrub mounds were assessed by placing a steel rod on top of the shrub mound, parallel to the interspace soil surface, and measuring the distance between the rod and the soil surface. In addition, we measured plant cover, in six 1 m^2 quadrats placed in the interspaces, using a point frame with a grid of 100 crosshairs, and the average height of five randomly chosen plants for each species. All plants within the quadrats were clipped at ground level, separated into species, oven-dried at 65 °C for 48 h and weighed to determine aboveground biomass.

Soil chemistry and bulk density

Samples of soil were collected from the surface 20 cm from the 92 shrub locations and their adjacent (paired) interspaces. Shrub soils were collected adjacent to the stem and interspace soils about 2 m from the edge of the shrubs. Four samples were selected in each microsite, bulked, air dried, ground and sieved to <2 mm. Soil organic C content was determined using the dichromate oxidation method. Total nitrogen (N) was determined using semi-micro Kjeldahl method, and total phosphorus (P) using the molybdenum antimony resistance-colorimetric method (Bao 2000). Soil bulk density was measured in the top 20 cm using a 100 cm^3 steel corer. Gravimetric soil moisture determined after drying the samples at 104 °C for 48 h.

Statistical analyses

Our data were checked for normality and homogeneity of the residuals using Levene's Test prior to analyses. A Student t-test was used to compare the effects of the two microsites (shrub, interspace) on vegetation characteristics, soil bulk density, soil organic C, total N, and total P in the five sites, and one-way analysis of variance (ANOVA) used to compare the effects of the five different grazing treatments on vegetation characteristics, soil physical and chemical indices, and differences examined using Least Significant Difference (LSD) tests. Relationships among shrub mound height and soil bulk density, organic C and nutrients in the two positions and five sites were tested using exponential models for model selection based on corrected Akaike Information Criterion (AICc).

We used the relative interaction intensity (RII, Armas et al. 2004) to estimate the magnitude of the shrub patch effect on bulk density, and soil C, N and P. The RII was calculated as: $RII = (X_{Shrub\ patch} - X_{Interspace}) / (X_{Shrub\ patch} + X_{Interspace})$, where X is the value of a given attribute, e.g. soil C. This index ranges from −1 to 1, with RII values >0 indicating relatively greater values in the shrub patches than the interspaces.

We then used Structural Equation Modeling (SEM; Grace 2006) to examine the effects of shrubs, mound height, grazing intensity, bulk density and plant cover on three soil variables; soil organic C, and total N and P. Our a priori model predicted that grazing and bulk density, and to a lesser extent shrub mound height, would have strong negative effects on our three soil variables whereas shrubs would have a positive effect. We compared our a priori model with our data variance-covariance matrix to assess an overall goodness-of-fit, using the χ^2 statistic. The goodness of fit test estimates the probability of the observed data given the a priori model structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 24 (IBM, Chicago, IL, USA) software. The model with the strongest measures of fit (e.g., low χ^2, high Goodness of Fit Index [GFI] and high Normal Fit Index [NFI]) was interpreted as showing the best fit to our data. The strength and sign of relationships among the variables is represented by path coefficients, which are analogous to partial correlation coefficients (Grace 2006).

Results

Plant community properties and shrub mound height

Groundstorey plant cover and height within shrub patches at the two long-term ungrazed (LU, MU) sites were significantly greater than those of recently ungrazed (RU) and overgrazed sites (MO, EO) ($F_{4, 87} = 24.03$, $P < 0.001$; Table 1). Shrub mound height increased gradually from long-ungrazed to extremely overgrazed.

Soil properties in relation to grazing site and patch type

In general, soil bulk density was always lower in the shrub patches whereas organic C, total N and total P were always greater in soils beneath shrub patches than interspace (Fig. 1). Soil bulk density increased with increasing grazing intensity from long ungrazed to extremely overgrazed, and the trend was consistent for both shrub hummocks and interspaces (Fig. 1). Conversely, soil organic C, total N and total P showed the opposite trend, with the most pronounced differences occurring between the two ungrazed sites and the grazed sites for both shrub patches and interspaces (Fig. 1).

Increasing shrub mound height was associated with exponential increases in soil bulk density under shrubs and in the interspaces, and the rate of increase was more pronounced in the interspaces. Soil organic C, total N and total P showed the opposite trend, declining with

Table 1 Mean (± SE) values for community properties and shrub mound height for the five sites

Site	n	Shrub patch			
		Patch area (m^2)	Mound height (cm)	Shrub height (cm)	Plant cover (%)
LU	16	6.8 ± 1.29^{ab}	2.4 ± 0.48^{e}	55.3 ± 3.39^{a}	68.2 ± 3.56^{ab}
MU	20	5.4 ± 0.64^{b}	5.6 ± 0.55^{d}	57.4 ± 2.77^{a}	71.0 ± 2.58^{a}
RU	18	7.2 ± 1.38^{ab}	11.1 ± 0.75^{c}	41.1 ± 2.36^{b}	70.6 ± 3.10^{a}
MO	18	9.9 ± 1.78^{a}	14.7 ± 0.76^{b}	35.2 ± 1.36^{b}	59.8 ± 2.26^{b}
EO	20	5.5 ± 0.63^{b}	24.1 ± 1.36^{a}	26.9 ± 1.63^{c}	41.2 ± 2.59^{c}

Sites: Long ungrazed (35 years; LU); Moderately ungrazed (19 year; MU); Recently ungrazed (2 years; RU); moderately overgrazed (MO); extremely overgrazed (EO). Within a given patch type, different letters indicate a significant difference in the attribute at $P < 0.05$

increasing shrub mound height, with the strongest decline in the interspaces (Fig. 2).

We found that, compared with the interspaces, the relative magnitude (RII) of soil C and nutrients in the shrub patches was greatest in the moderately overgrazed site. This effect, however, collapsed at both extremely overgrazed and long ungrazed (Fig. 3). Sites of the RII for soil C, N and P exhibited a unimodal response to changing shrub mound height, with very low values for short and tall mounds (RII < 0.1) and high values (RII = 0.2–0.3) for shrub mounds of intermediate height (Fig. 4). Bulk density showed a similar unimodal response.

Direct and indirect effects of grazing and shrubs on nutrients

Our structural equation models explained a substantial amount of the variance in organic C, total N and total P.

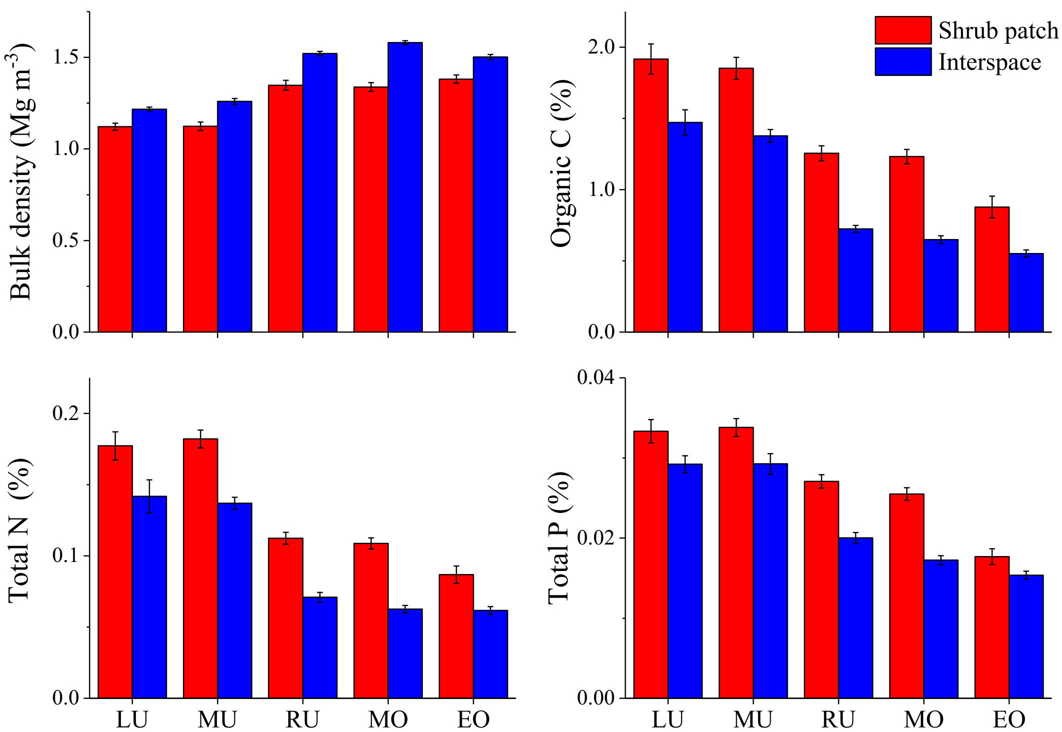

Fig. 1 Mean (± SE) values for soil bulk density, organic carbon, total nitrogen and total phosphorus (0–20 cm) under shrubs and in the interspaces across the five sites. Sites: Long ungrazed (35 years; LU); Moderately ungrazed (19 year; MU); Recently ungrazed (2 years; RU); moderately overgrazed (MO); extremely overgrazed (EO). Positions: Shrub patch and Interspace. There are significant differences in positions (shrub patch and interspace) for all attributes and grazing scenarios at $P < 0.05$

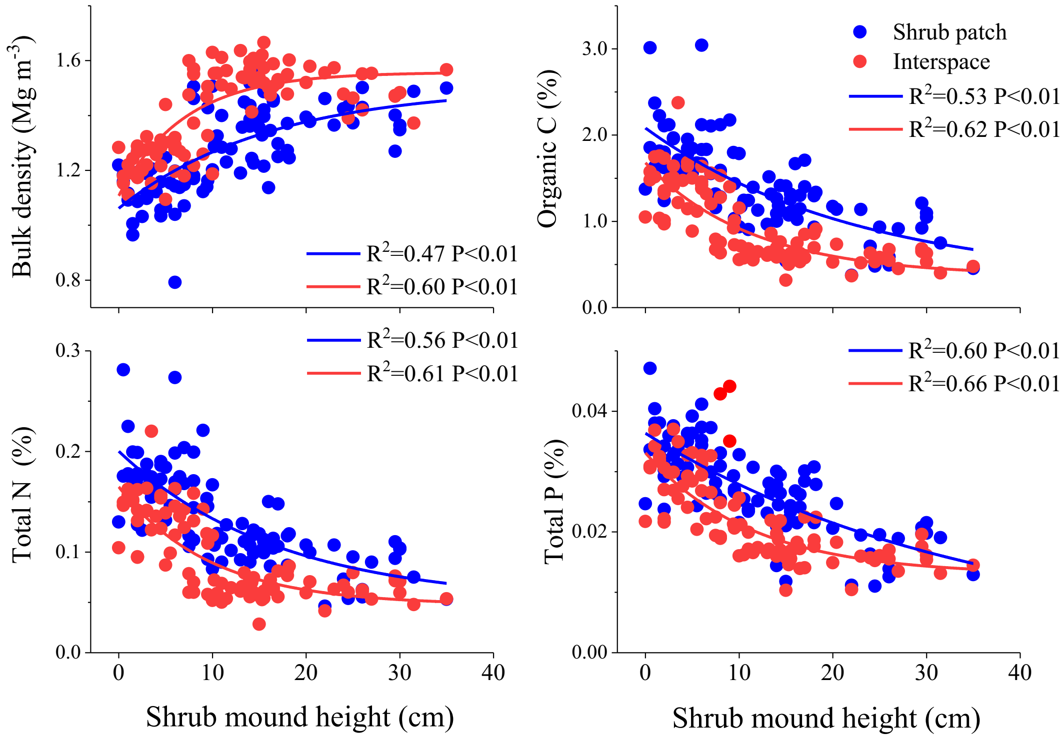

Fig. 2 Trends in soil bulk density, organic C and total N and P in the top 20 cm with increasing shrub mound height. Positions: shrub patch and Interspace

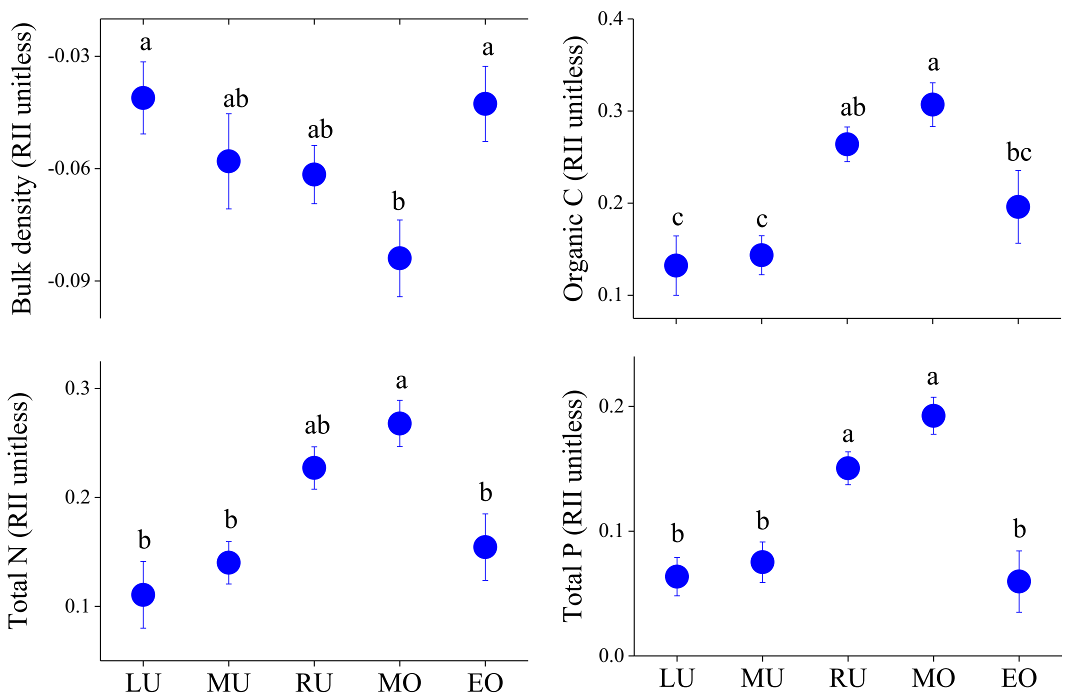

Fig. 3 Mean (± SE) relative interaction intensity (RII) for soil bulk density, organic carbon, total nitrogen and total phosphorus in the surface 20 cm under five grazing sites. Sites: Long ungrazed (35 years; LU); Moderately ungrazed (19 year; MU); Recently ungrazed (2 years; RU); moderately overgrazed (MO); extremely overgrazed (EO). Within a given patch type, different letters indicate a significant difference in the attribute at $P < 0.05$

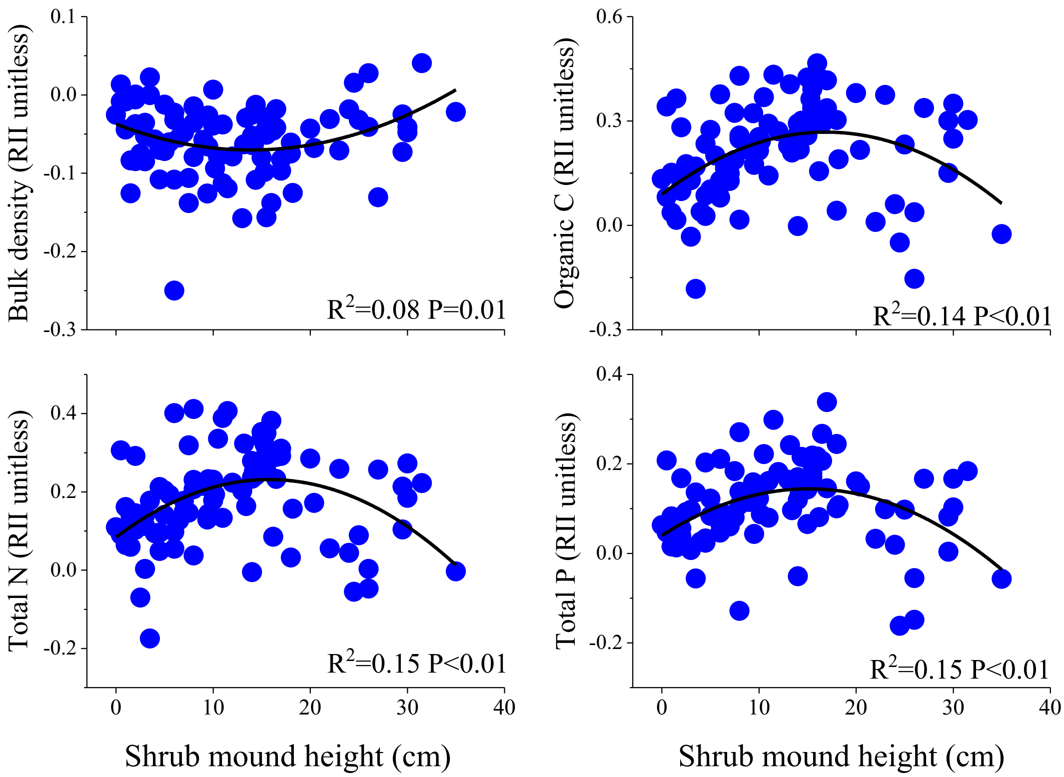

Fig. 4 The relative interaction intensity (RII) in relation to shrub mound height (cm) for soil bulk density, organic carbon, total nitrogen and total phosphorus in the surface 20 cm under five sites

Our models showed that grazing and bulk density, and to a lesser extent shrub mound height, had strong negative effects on soil organic C (Fig. 5b), total N (Fig. S1a) and total P (Fig. S1b), whereas shrubs had a positive effect on organic C, total N and total P (Fig. 5b; Fig. S1a, S1b). Part of the mechanism underpinning the negative effects of grazing was either by enhancing the negative effect of bulk density, or by increasing the negative effect of mound height on soil organic C. Apart from the positive effect of shrubs on organic C, total N and total P, shrubs suppressed the negative effects of bulk density on organic C.

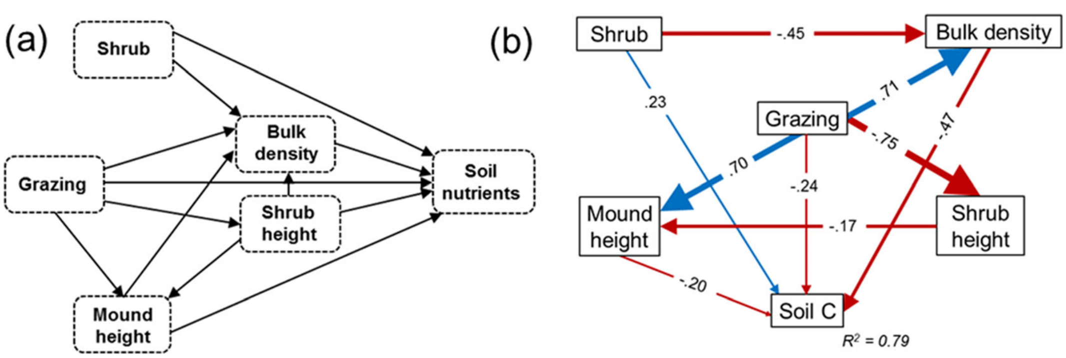

Fig. 5 Structural equation models describing the effects of multiple drivers (Shrubs, mound height, Grazing intensity, Grazing, Bulk density and Plant cover on soil nutrients. (**a**) a priori model, (**b**) model for soil carbon. Arrows indicate the direction of the effect. The numbers adjacent to arrows, path coefficients, which are analogous to partial correlation coefficients, are indicative the effect size of the relationship and may be positive (blue) or negative (red). Only significant ($P < 0.05$) pathways are shown the proportion of variance in soil carbon (R^2) is given. Model fit: $\chi^2 = 0.02$, df = 1, $P = 0.98$, GFI = 1.00, RMSEA = 0.001, Bollen-Stine = 0.96

Discussion

Increasing grazing intensity is associated with reduced soil function

Livestock grazing is one of the most pervasive global land uses on Earth, occupying more than a quarter of the terrestrial land surface (FAO 2014). Grazing can have direct and indirect effects on ecosystem properties and processes, as broad as altering plant cover and composition through herbivory, disturbing surface soils, changing soil insolation, destabilizing topsoil, and accelerating wind and water erosion (Eldridge et al. 2017; Yan et al. 2018). In our study, soil C, N and P functions declined substantially with increasing grazing intensity, which was associated with less plant cover and biomass, shorter plants, and substantial reductions in the mass of surface litter, particularly at continuously overgrazed sites (Table S1). Furthermore, sites subjected to heavy grazing had more compacted soils with lower levels of organic C, N and P than long ungrazed sites.

In our structural equation models, we observed some indirect effects of increasing grazing (Fig. 5). Grazing was expressed through the negative effect of bulk density on soil organic C and nutrients. Higher bulk density under grazing is likely due to trampling by livestock, and reductions in belowground biomass (Hao et al. 2018; Heggenes et al. 2017; Su et al. 2004). Indirectly, however, bulk density would also be likely to increase with reductions in surface cover simply due to greater soil insolation and fewer inputs of litter into the soil and therefore lower populations of soil-borne invertebrates, that are important for promoting soil porosity (Román-Sánchez et al. 2018; Will and Suter 1995). Increased soil bulk density would also likely reduce root growth and therefore lead to lower levels of soil organic C and nutrient accumulation (Conforti et al. 2016; Telles et al. 2004).

Grazing increased the negative effect of shrub mound height on soil organic C, N and P (Fig. 5). Shrub mound height was higher in continuously overgrazing sites than under extended grazing exclusion (Table 1), suggesting the accretion of sediment due to overgrazing. Although we did not measure wind erosion, there is strong support for the notion that wind erosion is directly related to increasing mound height and reductions in soil organic C and nutrients. Shrub patches can effectively reduce wind erosion and intensify the capture of sediments compared with the interspaces due to differences in vegetation cover. Thus the mounds beneath shrubs could accrete due to increasing sediment production in the interspaces (Tengberg 1995). Rates of wind erosion in our study area are about 0.43 kg m^{-2} min^{-1}, about 11-times that of long-term ungrazed grasslands (0.04 kg m^{-2} min^{-1}) (Yan et al. 2011). We have previously shown that overgrazing increases the proportion of sand (> 0.05 mm diameter) in the soil (Yan et al. 2013) and that soil organic C, total N and total P decline with increasing sand content (Yan et al. 2013). Greater sand content would likely equate with increasing mound height given the contribution of saltating particles to mounds. It is likely, therefore, that wind erosion, which is associated with overgrazing, contributes not only to a greater mound height, but to reductions in soil organic C and nutrients in our study. Sediment deposition by water erosion is unlikely to be a causal mechanism for mound accretion because our sites are relatively flat and run-off events are low. Indeed, water erosion would be expected to have the opposite effect by reducing mound height through splash erosion (Bonell et al. 1986).

We also found lower concentrations of total P under grazing, which seems at odds with current models of P formation. Phosphorus is under abiotic control and is derived largely from subsoil, a major source of ecosystem P (Delgado-Baquerizo et al. 2013), but it is also cycled through vegetation. Animal dung is also a significant source of P (Cournane et al. 2011), so we might have expected to have detected increases in P with increased grazing. The most parsimonious explanation is that grazing results in a net export of P from shrubland sites by exacerbating the removal of organic matter or by increasing wind erosion (Sparrow et al. 2003). Consistently lower levels of plant biomass and the absence of litter under heavy grazing compared with exclosure (Table S1), which is consistent with other studies in of overgrazed shrublands (Eldridge et al. 2015), would exacerbate any return to the soil of P recycled in vegetation.

Positive effects of shrubs on resources collapse under extremely grazing

Woody plants have marked impacts on understorey vegetation and are known to concentrate resources under their canopies (García-Moya and McKell 1970; Ochoa-Hueso et al. 2018; Schlesinger et al. 1990; Weltzin and Coughenour 1990). We assessed the relative importance of shrubs as sinks for soil C and nutrients by calculating the relative interaction intensity index (RII) of nutrients under different grazing scenarios. A zero value of RII represents a point at which the relative shrub effect on resources is equivalent to the relative effect of the interspaces. Our results indicate that the relative importance of shrubs increases from long ungrazed to long moderately overgrazed, but that this effect collapses under extreme levels of grazing. Thus, for example, the relative effect of shrubs on soil N at the most extreme level of grazing was comparable to that under a long-ungrazed scenario, though total pools were likely substantially different. The relative shrub affect declined to almost zero under extreme overgrazing, potentially due to the winnowing of fine material from the hummocks by wind, leaving a lag deposit of coarse material (Dougill and Thomas 2002) which is low in C and nutrients. Our work provides strong empirical support for the notion that the strength of the fertile island effect may be direct result of grazing (Allington and Valone 2014), with greater reductions in interspace conditions relative to those beneath the shrubs as grazing intensity increases.

The mechanisms underlying the shrub patch effect on resources may relate to shrub traits. For example, the shrubs in our study area, *Caragana microphylla*, are generally unpalatable to livestock (Yan et al. 2019), so plants and soils in the mounds would be protected from herbivory by associational resistance (Smit and Ruifrok 2011), leading to greater plant cover and therefore greater soil C concentrations (Han et al. 2008). We would also expect greater soil N beneath shrubs because *Caragana microphylla* fixes N (Yan et al. 2019). Further, semi-fossorial rodents such as *Microtus brandti,* construct their burrows within the shrub mounds (Su et al. 2016), and this can lead to increases in fertility due to increases in organic waste, infiltration and decomposition (Mallen-Cooper et al. 2018).

Our structural equation models indicate strong support for the notion that shrubs suppress the negative effects of bulk density on soil C and nutrients. Shrubs have been shown to reduce threshold wind velocities near the surface, causing finer-textured, wind-borne sediments rich in C and N to deposit out of the airstream, resulting in a resource-richer soil (Wezel et al. 2000) with improved soil structure, more abundant plant roots, and lower bulk density (Yang et al. 2011). Shrubs also become preferred habitat for soil invertebrates and microbes, and therefore biological hotspots (Bolton et al. 1993; Herman et al. 1995; Navarro-Cano et al. 2015), reinforcing their positive effects on soil porosity through the creation of biopores (Li et al. 2013).

We found strong evidence for exponential increases in soil bulk density, and declines in soil organic C, N and P, with increasing shrub mound height (Fig. 2), which has been shown to be highly correlated with the severity of wind erosion (Bochet et al. 2000; Hennessy et al. 1985). Further, intermediate levels of grazing intensity will be expected to mobilise fine particles by wind erosion (Yan et al. 2011, 2013), enhancing the relative shrub affect compared with situations where there is little or no redistribution of soil (ungrazed or long ungrazed). Extremely high levels of grazing, however, and the activation of high levels of wind erosion and the removal of fine, nutrient-laden sediments, will lead to an homogenisation of soil nutrient properties (Wiesmeier et al. 2009), suppressing the relative shrub affect. The maximisation of shrub effects at intermediate mound heights (~ 15 cm high) suggests that, at least in our study site, resource capture and the relative retention efficiency of shrubs is greatest at intermediate mound heights, which likely correspond to intermediate levels of grazing induced wind erosion.

Concluding remarks

Our results indicate that shrubs are critical elements of Eurasian grasslands, supporting soils that are more porous, and with greater levels of soil organic C, total N and total P. Furthermore, we showed that this positive effect of shrubs on soil functions are maximised at intermediate levels of grazing. Thus, soil function is reinforced by the presence of shrubs, at least under moderate levels of grazing. Grazing-induced disturbance is therefore a self-reinforcement process leading to the concentration of resources across a small area at the expense of a more extensive area of grassland. The extent to which shrubs and their supporting mounds persist after grazing exclusion is unknown, but considerable energy (e.g., herbicide, cutting, mowing) would be required for reversion of stable shrubland to the former grassland. We have demonstrated that the fertile island effect increases with increasing grazing-induced disturbance, providing further support for the notion that it is an artefact of overgrazing (Allington and Valone 2014). Low-level grazing of grassland, to mediate against shrub encroachment, soil nutrient movement from the interspaces and therefore the enhancement of any fertile island effect, would appear to be an appropriate strategy for maintaining healthy productive grasslands.

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Author's contribution Y. Y. designed the experiment; Y.C., Y.Y., D.X., C.W., and X.W. conducted the field work. Y.C., Y.Y. and D.J.E. performed the data analyses and wrote the manuscript, and all authors provided comments on the manuscript and the revisions and approved the final version.

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