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Response of ecosystem structure to shrub encroachment varies with the degree of encroachment

Jingyi Ding[1], Yi Han[1,2], Wenwu Zhao[1], Jian Hu[3], Xuan Gao[1], Yue Yan[1], Yijin Wang[4], David Eldridge[5]

1. State Key Laboratory of Earth Surface Processes and Disaster Risk Reduction, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.
2. Key Laboratory of Poyang Lake Wetland and Watershed Research (Ministry of Education), School of Geography and Environment, Jiangxi Normal University, Nanchang, 330022, China
3. Sichuan Zoige Alpine Wetland Ecosystem National Observation and Research Station, Southwest Minzu University, Chengdu 610041, China
4. School of Natural Resources, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China
5. Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney 2052, Australia.

Abstract

Grasslands are one of the major ecosystem types in drylands that support multiple ecosystem functions and human livelihoods. Encroachment of shrubs into grasslands affects the functioning of drylands by altering community structure, with impacts exacerbated under greater intensity of encroachment. Yet, we have a limited understanding of how ecosystem structure responds to the degree of shrub

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encroachment. Here, we describe a field-based study designed to examine changes in ecosystem structure beneath shrub patches (patch condition) and between patches (spatial distribution pattern of patches) along a gradient in encroachment in a semiarid grassland in Inner Mongolia, China. We used shrub cover as a proxy of the degree of shrub encroachment and found that greater encroachment was associated with wider and taller shrubs with more branches. As shrub encroachment intensified, the area beneath shrubs had more litter and was less exposed to grazing. The pattern of spatial distribution of patches was characterized by more discontinuous patches of vegetation and more bare ground as shrub encroachment intensified. Either patch condition or spatial distribution pattern of patches was shaped mainly by the magnitude of shrub encroachment (cover) rather than by the changes in the structure of individual shrubs (e.g., height, canopy width). Our study highlights the idiosyncratic response of ecosystem structure (patch condition and spatial distribution pattern of patches) to intensifying shrub encroachment, reinforcing the importance of considering the degree of shrub encroachment when managing encroached grasslands.

Impact Statement

Our study shows how ecosystem properties change along the encroachment gradient. As shrubs spread, individual patches become stronger “fertile islands” – the surface beneath them becomes rougher, collects more litter, and shrub size increases. However, increasing shrub cover simultaneously fragments the landscape, breaking connections between plant patches and creating a more disconnected environment. These opposing effects (better conditions beneath shrubs but reduced landscape connectivity) create significant trade-offs for the ecosystem and its inhabitants. This could include biota that operate at spatial scales consistent with the size of shrub patches. Conversely, animals needing larger open spaces (grassland specialists) or those forced to move longer distances between patches (such as mammals or some ground-nesting birds) are disadvantaged by the increased isolation and predation risk. Shrub encroachment is expected to intensify under drier, hotter conditions, amplifying this patchy landscape structure with fertile islands. Thus, the extend or encroachment

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is a critical consideration for managers. Moderate levels may present a balance for some benefits like biodiversity and carbon, while extensive encroachment favors shrubland species at the expense of grassland communities and overall landscape connectivity. Understanding the specific level of encroachment is therefore essential for predicting impacts and effectively managing these ecosystems under changing climates.

KEYWORDS

Climate change, Drylands, Encroachment stage, Patch condition, Spatial pattern

1. Introduction

Grasslands are a major biome in drylands, occupying 41% of the terrestrial area and accounting for 69% of global farmland (Suttie et al. 2005, O'Mara 2012). Grasslands support a large proportion of the world’s livestock and provide multiple ecosystem services such as climate regulation, soil conservation and biodiversity maintenance that are critical for human wellbeing (Bardgett et al. 2021). Yet, grasslands are threatened globally by increases in woody plants, largely a result of multiple interacting drivers including increasing land use pressures, greater atmospheric carbon dioxide concentrations and more varied rainfall events (Archer et al., 2017, Stanton et al. 2017, Ding & Eldridge 2024). Encroachment of woody plants into grasslands is likely to reduce not only pastoral potential, but lead to the widespread loss of critical ecosystem goods and services (Anadón et al. 2014, Archer et al. 2017). Encroachment by shrubs (shrub encroachment) is globally widespread, with current estimates of 500 billion km^2 affected (Eldridge et al. 2011, Deng et al. 2021). However, the functional effects of shrub encroachment are highly debated, with the encroachment enhancing the quality of soil and environmental conditions for plants but regarded as a sign of grassland degradation (e.g., Ward et al., 2018, Eldridge et al. 2024). The effect of shrub encroachment also varies with its extent, with heavily encroached sites generally impossible to revert to grassland (Anadón et al. 2014, Eldridge & Soliveres 2015). Predicted increases in climate variability are thought to stimulate shrub growth

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and therefore promote encroachment at the expense of grasslands (Deng et al. 2021, Bestelmeyer et al. 2018). The impacts of shrub encroachment on ecosystem functions and services are intimately tied to changes in ecosystem structure. Thus, a better understanding of the response of ecosystem structure to intensifying shrub encroachment is essential if we are to effectively manage encroached grasslands under changing climates and land uses.

Despite the numerous studies of encroachment impacts on ecosystems, there is still considerable debate about the relative benefits or disbenefits of shrubs for ecosystem structure (Eldridge and Soliveres 2015). This uncertainty is due to the fact that their effects on ecosystem structure depend on the level of ecological processes over which they are assessed (e.g., Okin et al. 2015). For example, wide canopies, deep roots, and branching stems of shrubs promote carbon and nutrient sequestration and hydrological function more effectively than herbaceous plants (Ward et al. 2018, Howard et al. 2012). The resource accumulation beneath shrub patches leads to the formation of fertile islands and biogeochemical hotspots (Eldridge et al. 2024) that provide refugia for plants and animals (Ochoa-Hueso et al. 2018, Ding & Eldridge 2020). Such a heterogenous distribution of resources beneath shrub patches would be expected to alter the spatial distribution of patches. For example, feedback between resource distribution and the development of shrub patches can lead to an acceleration of shrub encroachment, and a dwindling of resources in the interspaces, leading to self-perpetuating systems of resource-enriched islands within a resource-poor matrix (D'Odorico et al. 2012). This would affect the spatial distribution of vegetation patches, which can alter the flows of energy and resources within the system, thus affecting ecosystem functions across the entire encroached system (Okin et al. 2008, Okin et al. 2015). However, current encroachment studies have tended to focus on finer scale responses such as changes beneath patches (Maestre et al., 2010; Eldridge & Soliveres, 2015). The mechanisms by which ecosystem structure responds to shrub encroachment from finer (beneath patches) to coarser (between patches) levels remain

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poorly understood. Such a knowledge gap makes it more challenging to manage grassland functions more effectively by regulating different levels of ecosystem structure.

The response of ecosystem structure to encroachment also varies with the degree of encroachment (Eldridge & Soliveres 2015). When shrub cover is sparse, at low degree of encroachment, forage production could potentially be greater under encroachment due to the addition of novel niches that support a larger range of plant species (Howard et al. 2012). As shrub cover increases, the larger canopy cover and deeper root system of shrubs would increase resource competition on herbaceous species and therefore reduce grass biomass (Brown & Archer 1989, Anadón et al. 2014). These changes in ecosystem attributes with the degree of encroachment are thought to reflect shifts in ecosystem status (Bestelmeyer et al. 2018). For example, vegetation biomass and plant richness have been shown to decline from low to medium encroachment but increase from medium to heavy encroachment, suggesting a state change from grass dominance to shrub dominance (Peng et al. 2013). These changes in ecological attributes arise potentially from changes in shrub community characteristics (canopy, height, size distribution) as shrubs expand (Maestre et al. 2016). However, as most studies to date have tended to focus on a particular degree of encroachment (e.g., low, medium, or heavy), empirical evidence for change across a wide spectrum of encroachment is lacking (Peng et al., 2013; Soliveres & Eldridge, 2013), making it difficult to manage grasslands under different levels of encroachment, particularly during the early stages of encroachment when woody removal treatment is more effective (Ding & Eldridge, 2024) and financially viable.

To address these issues, we analyzed the response of ecosystem structure beneath patches (patch condition) and between patches (spatial distribution pattern of patches) along an extensive shrub encroachment gradient covering low, medium and heavy encroachment sites across Inner Mongolia, China. Regression analyses, linear models

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and structural equation modeling were used to address three predictions. First, we expected that for ecosystem structure beneath patches (Fig. 1a), community structural characteristics (e.g., height, canopy) would vary with the degree of shrub encroachment, and soil and vegetation condition (e.g., litter, crust stability, exposure to grazing) would become more stable in the shrub patch as shrub encroachment intensifies due to the accumulation of resources beneath shrubs. Second, we predicted that for ecosystem structure between vegetation patches (i.e., spatial distribution patterns of vegetation patches), connectivity among vegetation patches would decline with increasing shrub encroachment (Fig. 1b). This is because increasing shrub encroachment would result in the aggregation of shrubs, which strengthens resource redistribution from the grassy interspaces to the aggregated shrub patches, thus leading to a more discrete and broken landscape. Third, for those mechanisms promoting ecosystem structural changes under intensified shrub encroachment, we expected that increasing degree of shrub encroachment would elicit changes in the spatial pattern of patches. This would be expected to occur either directly or indirectly, by altering ecosystem structure beneath patches (e.g., community characteristics of shrubs such as height, canopy width and patch condition). Such effects would be enhanced under drier and hotter climatic conditions (e.g., greater aridity and mean annual temperature). This is because changes in community- and patch-level structure would alter resource redistribution at the site or landscape level, thus regulating the organization of vegetation. Further, the effect of encroachment is known to strengthen in drier and hotter environments.

2. Methods

2.1 Study area

This study was conducted in Xilingol, Inner Mongolia, China, in the central part of the Eurasian steppe (Fig. 2). We established an east-west transect (43.92° N ~46.56° N; 113.54° E~119.29° E) of shrub encroached grasslands across typical steppe. The mean annual temperature of the study area ranges from 0 to 3 °C and mean annual

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precipitation from 150 to 500 mm. Soils in the area are dominated by chernozems, and typical and sandy chestnut soils. The dominant grass species are *Stipa baicalensis*, *Filifolium sibiricum*, *Stipa krylovii*, *Stipa grandis* and *Stipa klemenzii*, and the dominant encroached shrub species is *Caragana microphylla*. To avoid the confounding effect from human disturbance and additional water resources, all the study sites were selected away from any towns, villages and rivers.

2.2 Field survey

2.2.1 Vegetation sampling

We surveyed 30 sites along the gradient of shrub encroachment across semiarid and arid areas in August 2022 (Fig. 2).

In each site, we established a 30 m x 30 m sampling plot within which we measured four structural measures of 20 shrubs: 1) height (cm); 2) canopy width (cm); 3) stem diameter (cm); and 4) the number of branches. This allowed us to assess the community structural characteristics of shrubs (Hypothesis 1). Shrubs were selected randomly across the whole 30 m x 30 m plot. We counted the number of shrubs to derive a measure of shrub density, and measured all shrubs at sites supporting fewer than 20 shrubs. To better capture the distribution of shrubs, shrub cover was estimated using drone image from DJI Mavic 2 (resolution 1.4 cm; See 2.2.3 for details). In each site, we selected a 30 m x 30 m image corresponding with the field-based sampling plot and used a line intercept method to estimate shrub cover in each site. In encroached grassland of Inner Mongolia, shrub cover peaked at ~40%, with *Caragana* spp. being the major encroached species (Chen et al., 2014). In our study, shrub cover in the 30 sites ranged from 0.5% (low encroachment) to 37% (heavy encroachment), which spanned the entire range of encroachment in the region, covering low, medium and high degree of encroachment. However, the range of encroachment may not be equivalent to that in other areas across the globe due to differences in woody species and ecosystem biomes (Eldridge & Soliveres, 2015).

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2.2.2 Soil surface condition assessment

To assess patch condition beneath shrubs and grasses (Hypothesis 1). we measured 13 soil surface attributes within a 0.5 m x 0.5 m quadrat beneath five replicate shrubs and within their paired grassy interspace in each plot. Soil surface condition is strongly related to ecosystem functions (e.g., infiltration, nutrient, microbial activities; Ding et al., 2022; Eldridge and Delgado-Baquerizo, 2018). Within each quadrat, we assessed (1) crust resistance, (2) crust brokenness, (3) crust stability, (4) the cover of biocrusts, (5) cover of deposited material, (6) erosion cover, (7) surface roughness, (8) grazing intensity, by measuring the mass of dung of different herbivores, (9) basal cover, (10) foliage cover, (11) plant richness, (12) litter cover, and (13) litter depth using a modified version of the Soil Surface Condition protocols used in the Landscape Function Analysis procedure (LFA; Tongway and Hindley, 2004, Eldridge et al., 2020a, see details and measurements for each attribute in Table 1). After assessing soil and vegetation conditions, we clipped all of the understorey plants in each 0.5 m x 0.5 m quadrat, and oven dried the material at 65°C for 48h to measure herbaceous biomass as a measure of forage production.

2.2.3 Drone image processing

We used a drone to obtain high resolution images of each site to assess spatial distribution pattern of patches. A DJI Mavic 2 (Da-Jiang Innovations, Shenzhen, China) was used to capture high spatial resolution (1.4 cm pixels) visible colour imagery in an 8-bit jpeg format of the site. Each site was flown in an area of 100*100 m in a series of parallel flight paths (Designed by DJI GS Pro APP) at a height of 15 m above ground level. The OpenDroneMap software program was used to process images from each field site into an 8-bit ortho-mosaic geo-referenced geo-tiff image. OpenDroneMap is a free open-source UAV photogrammetry software platform that is run in a virtualisation with docker container environment.

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To assess landscape connectivity (among vegetation patches), we classified the whole site into two land cover types, vegetation and bare ground, in ENVI 5.5 (https://envi.geoscene.cn/) using support vector machine classification based on the DJI Mavic 2 high spatial resolution image. We classified the image into vegetation and bare to assess the vegetation connectivity between patches.

2.3 Statistical analysis

2.3.1 Variation in shrub community

To obtain the community characteristics of shrubs at each 30 m x 30 m plots, we calculated the mean, median, skewness (degree of asymmetry) and kurtosis (the tailedness) of the size distribution, and the coefficient of variation (CV%) of canopy width, height, stem diameter and number of branches of each shrub at a site. We then fitted linear regressions between measures of community structure and the square root of shrub cover to explore how shrub community changes with the degree of shrub encroachment.

2.3.2 Difference beneath patches

To assess the spatial distribution pattern of patches (Hypothesis 2), we used one-way ANOVA to compare the differences in soil surface condition between shrub patches and interspaces. We fitted linear regression and quantile regression (5^{th}, 95^{th} quantile) between measures of soil surface condition and the square root of shrub cover to explore whether the conditions of the shrub and interspace grassy patch changed significantly with increasing shrub encroachment. Quantile regression is used widely in ecology to illustrate changes in linear relationships and to quantify the boundaries of scatter points against environment gradients (Scharf et al. 1998).

To assess the spatial variation in soil surface conditions at each 30 m x 30 m plot, we calculated a dissimilarity index (Bray-Curtis dissimilarity, unitless) between shrub the patch and paired interspace based on the matrix of attributes (raw values) within

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different components of the soil surface; i) the surface crust (crust resistance, crust brokenness, crust stability, the cover of biocrusts), ii) other surface attributes (cover of deposited material, erosion cover, surface roughness, grazing intensity), and iii) plant attributes (basal cover, foliage cover, plant richness, litter cover, litter depth). We then used average dissimilarity as a measure of spatial variability at each site. The Bray-Curtis dissimilarity between vegetation patch type *j* and *k* at each site (D_{jk}) is calculated as

$$D_{jk} = \sum_{i=1}^{n} |x_{ij} - x_{ik}| / \sum_{i=1}^{n} (x_{ij} + x_{ik}) \quad (1)$$

where x_{ij} and x_{ik} are the raw values of soil attributes *i* in vegetation patch type *j* and *k* at each site. *n* is the number of soil surface attributes.

2.3.3 Vegetation distribution pattern assessment

To assess the spatial distribution pattern of patches, we selected eight landscape pattern indices that describe the brokenness of connectivity of vegetation patches compared to the non-vegetated patches (ecological meaning and rationale of indices selection is shown in Supplementary Table S1):

(a) Aggregation Index (AI, %).

$$\text{AI} = \left[\frac{g_{ii}}{max \to g_{ii}}\right] * (100\%) \quad (2)$$

g_{ii} is number of similar adjacencies (joins) between pixels of patch type (class, vegetated *cf.* bare) *i* based on the single-count method. $max \to g_{ii}$ is the maximum number of similar adjacencies (joins) between pixels of patch type (class) i (see below) based on the single-count method. The index ranges from 0 to 100, with greater number indicating more aggregation of the patch type.

(b) Standard Deviation of Patch Area (unitless). Standard deviation of the patch area. An index > 0 indicates a more variable patch size.

(c) Edge Density (m/m^2). This is the sum of the lengths of all edge segments in the landscape, divided by the total landscape area. An index value > 0 indicates greater patch brokenness.

(d) Landscape Division Index (DIVISION, unitless).

$$\text{DIVISION} = \left[1 - \sum_{j=1}^{n} (\frac{a_{ij}}{A})^2\right] \quad (3)$$

a_{ij} is the size of patch ij. A is the total landscape area. The index ranges from 0 to 1, with a greater number indicating more patch brokenness and landscape complexity.

(e) Landscape Shape Index (LSI, unitless).

$$\text{LSI} = \frac{0.25E}{\sqrt{A}} \quad (4)$$

E is the total length (m) of edges in the landscape and A the total landscape area. An index value > 0 indicates a greater degree of regularity in patch shape.

(f) Largest Patch Index (%). The percentage of the area of the largest patch in relation to total landscape area. The index ranges from 0 to 100, with greater number indicating that the landscape is dominated by larger patches.

(g) Patch Density (m/m^2). The number of patches of either vegetated or bare divided by total landscape area. A greater value of the index indicates lower landscape heterogeneity.

(h) Percentage of Landscape (%). The percentage of the area of a particular patch in relation to total landscape area. The index ranges from 0 to 100, with greater number indicating a greater dominance of that patch type in the landscape.

Landscape indices were calculated using Fragstats 4.2.1(https://fragstats.org/). Skewness was calculated from the 'moments' R package (Komsta & Novomestky, 2015). Figures were created using 'ggplot2' packages (Wickham, 2016) in R 3.4.3 version (R Core Team 2018).

2.3.4 Structural equation model

We used Structural Equation Modelling (SEM; Grace, 2006) to assess the mechanisms most highly related to ecosystem structure (Hypothesis 3). Structural Equation Modelling is used to explore the direct and indirect effects of the degree of encroachment on ecosystem structure (patch condition and vegetation distribution pattern), with climate and shrub community characteristics acting as covariates to take into account other confounding factors. In the *a priori* model (Supplementary Fig.

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S1), we predicted that climate would have direct effects on ecosystem structure, as well as indirect effects mediated by the degree of shrub encroachment, shrub community characteristics. We expected that the magnitude of encroachment would either directly affect ecosystem structure or exert indirect effects by altering shrub community characteristics. Overall goodness-of-fit probability tests were performed to determine the absolute fit of the best models, using the χ^2 statistic. The best fit model was selected with low χ^2 and Root Mean Error of Approximation (RMSEA < 0.05) and high Goodness of Fit Index (GFI) and R^2. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

3. Results

3.1 Variation in shrub community characteristics and patch condition with greater shrub encroachment

The structure and the size distribution of shrub communities varied markedly with increasing encroachment (Fig. 3). Shrub abundance generally increased with shrub encroachment. Shrubs tended to be larger, characterized by taller stems, wider canopies and more branches as shrub encroachment increased (P<0.05). Shrub size generally became more variable (canopy size, number of branches) in heavily encroached sites.

Across the encroachment gradient, the surface beneath shrubs had more and thicker litter than within grass patches (P<0.05, Fig. 4a). The soil surface was marginally rougher in shrub patches than grass patches, which were less exposed to grazing and therefore had slightly less dung as encroachment intensified, though not significant (Fig. 4b). Beneath the grass, crust stability declined markedly (P<0.05) as encroachment intensified (Fig. 4b). We found no evidence of significant dissimilarity in soil and vegetation attributes between shrub and grass patches in relation to intensifying encroachment (Supplementary Fig. S2).

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3.2 Variation in spatial distribution patterns of patches with greater shrub encroachment

The spatial organization of vegetation and bare patch varied with increases in shrub cover (Fig. 5). Increasing encroachment and therefore greater shrub cover was associated with more broken vegetation patches, with greater landscape division (*P*=0.062, marginal significant). Conversely, the size of bare patches increased with increasing encroachment, with declines in patch density (*P*=0.059) but increases in large patch index (*P*=0.063, marginal significant)

3.3 Impact of shrub encroachment on patch condition and spatial distribution pattern of patches

We further explored the mechanisms of shrub encroachment on influencing patch condition and the spatial distribution of patches (Fig. 6). We found that community structure and patch condition were both related to the degree of encroachment. Greater shrub abundance was associated with reduced shrub structure (shorter and narrower plants), but enhanced soil surface roughness beneath shrub patches. Conversely, greater shrub cover or abundance enhanced shrub structure (height and canopy) but reduced patch dissimilarity among shrub and the interspaces. Although the spatial distribution pattern of patches was not significantly related to factor, the degree of shrub encroachment (abundance, shrub cover), and shrub community structure (canopy) were major driving factors (Fig. 6b). For climate variables, mean annual temperature played important role in driving both patch condition and spatial pattern, with higher temperature enhanced surface roughness under shrub patches, intensifying landscape brokenness (higher landscape division value) and reduced the proportion of large patches (low large patch index value).

4. Discussion

Our study provides strong empirical evidence that the response of ecosystem structure to shrub encroachment varies with the degree of encroachment. As shrub

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encroachment intensified, the soil surface condition beneath shrub patch supported more litter, was exposed to less grazing, and the site comprised larger bare patches. Moreover, we found that both patch condition and spatial distribution pattern of patches was shaped mainly by the magnitude of shrub encroachment (cover) rather than through the changes in characteristics of shrub communities. Overall, our work reveals the response of ecosystem structure to intensifying shrub encroachment. Thus, studies of shrub encroachment and efforts to manage shrub encroachment need to be cognizant of the development stages of shrub encroachment.

Response of ecosystem structure depend on the degree of shrub encroachment

Our results indicate that the response of patch condition and spatial distribution pattern of patches significantly changes with the degree of shrub encroachment. For the condition beneath shrub patches, there is greater accumulation of litter, less exposure to grazing, and dominance of a less stable soil crust as shrub encroachment intensifies. This can be explained by distinct plant traits. Shrubs are long-lived and have woody stems, wide canopies, relatively unpalatable leaves, and deep root that can make it difficult for herbivores to penetrate the clumps (Westoby 1979). As encroachment intensifies, these shrubs form dense patches that are more resistant to grazing disturbance. Moreover, shrubs have a competitive advantage over grasses as climate become more variable (Knapp et al. 2008b, Archer et al. 2017, Kühn et al. 2021). The transfer of fine, nutrient-rich sediments from poorly vegetated grazed interspaces into shrub canopies through processes of wind and water erosion (Ravi et al. 2011, D'Odorico et al. 2012) reinforces islands of fertility (fertile islands) beneath shrub. These biogeochemical hotspots (Eldridge et al. 2024) also act as refugia for plants and animals against climate extremes and physical disturbance (Dean 1999, Ward et al. 2018). Conversely, herbaceous plants in the interspaces are both grazed and abraded by aeolian sediments (Li et al. 2022), thereby supporting both a less stable and more broken soil crust. These effects would likely intensify with increasing encroachment due to the lower availability of forage plants under conditions of

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greater shrub dominance.

Compared with the positive effect on ecosystem structure for patch condition, we found that increasing encroachment was associated with reduced landscape connectivity (i.e., the connectivity among vegetation patches) due to the heterogeneous distribution of resources that characterize patchy landscapes. This can be explained by the self-sustaining cycling of resource redistribution driven by the interactions among hydrological and aeolian processes, and fire regimes in drylands (Okin et al. 2015, Li et al. 2022). In grasslands, erosion processes redistribute water and soil resources from grass to shrub patch, with the greater capacity of nutrient scavenging by shrubs further reinforce such resource heterogeneity, thereby forming fertile islands beneath shrubs (D'Odorico et al., 2010). The dominance and coalescence of fertile islands leads to the development of a large “resource-sink” pattern (Chen et al. 2008). This pattern is maintained by processes of redistribution of resources driven by wind and water analogous to the fertile island phenomenon (Ying et al. 2017). Exacerbated by regional droughts, soil erosion, resource depletion, and vegetation loss surrounding large woody aggregations, reinforce the establishment and expansion of shrubs, forming self-sustaining cycles of resource redistribution, contributing to the irreversible transition from grass-dominated to shrub dominance system (Scheffer et al. 2012, Bestelmeyer et al. 2018). A widely studied examples of this phenomenon is embodied in the shrubland desertification paradigm of south-western USA (Schlesinger *et al*. 1990).

Contrary to our third hypothesis, we failed to detect any evidence of an impact of shrub encroachment on the spatial distribution pattern of patches via influencing patch condition. This could potentially be due to interactions with endogenous drivers between patches. For example, declines in forage availability can lead to more concentrated grazing of limited herbaceous material in an effort to compensate for the loss in livestock production (van der Koppel et al. 2002). Furthermore, reductions in

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grasses in the interspaces under grazing and drought would disconnect herbaceous fuel pathways, thus reducing fire frequency in grasslands and favouring the expansion of shrubs (Hodgkinson, 1998). Consequently, a continuous grassland landscape is replaced by a mosaic of shrub patches, which reduce the structure connectivity of the landscape and therefore the transfer of material among landscape elements (Larsen et al. 2012, Turnbull and Wainwright 2019). Such an effect would be strengthened under hotter climatic conditions, with higher mean annual temperature exacerbating the fragmentation of vegetation patches (higher landscape division value) and reduced the proportion of large patches. Hotter conditions would promote evapotranspiration and reduce water availability, which would give shrubs a competitive advantages over grasses due to their deeper root systems (Deng et al., 2021). This would lead to an intensification of shrub expansion and produce a more fragmented landscape.

Management implications

Increasing shrub encroachment changed vegetation structure beneath patches (e.g., greater fertile island effect) but resulted in reduced landscape connectivity by increasing patch isolation. Such contrasting effects are likely to have important impacts on shrubland- and grassland-dependent biota. For example, arthropods such as spiders that move and feed beneath patches in mixed grassland-shrubland systems would benefit from the edge effects that produce distinct foraging habitats (Daryanto & Eldridge 2012, Webb and Hopkins 1984). Shrub consolidation into larger patches will likely disadvantage these taxa by reducing surface heterogeneity within vegetation patches. Community composition of spiders has also been shown to vary with broader changes in land use change (e.g., forest converted to farmland; Major et al. 2006). Plant communities with diverse structures such as those with a greater variation in patch size or internal structure (height, configuration), provide a greater range of habitat, potentially favouring a wider species pool of spiders (Klimm et al., 2024). These beneficial effects from shrub patches would ensue with increasing shrub cover, consistent with studies showing that ant and beetle diversity increases with

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increasing shrub encroachment to at least 20% shrub cover (Blaum et al. 2009, Eldridge and Soliveres 2015). Yet, shrub encroachment is unlikely to benefit biota that operate at intermediate scales greater than shrub-interspace distances, with higher predation costs for animals that need to move between shrubby and open habitats (Brown *et al*. 1994). Further, there are likely to be major tradeoffs when evaluating the encroachment effect at the broader level, with encroachment sites favouring shrubland-obligate at the expense of grassland-obligate taxa (Coffman *et al*. 2014).

Moreover, the effect of encroachment on ecosystem structure depends highly on the degree of encroachment, with greater encroachment associated with healthier patch conditions but less connectivity among patches. The “regime shift hypothesis” suggests that as shrub encroachment intensifies, grassland ecosystems transition from a stable herb-dominated state to a shrub-dominated state, which alters ecosystem functions by altering ecosystem structure (Peng et al., 2013). Empirical studies reveal that moderate encroachment supports a greater species and functional diversity (Ding et al., 2020). Furthermore, synthesis studies reveal that ecosystem productivity peaks at ~15% shrub cover, while carbon sequestration peaks at ~30% cover (Eldridge and Soliveres, 2014). Thus, the extent of encroachment is critical important, and will determine the options available for shrub removal and the likely impacts of shrubs on ecosystem functions.

Conclusion

Our study provides novel evidence that the response of ecosystem structure to shrub encroachment depends on the degree of encroachment. The soil surface beneath shrubs was rougher, had more litter, and the shrubs were typically larger as encroachment expands. Conversely, connectivity collapses under shrub aggregation resulting in a more fragmented landscape. Furthermore, our study demonstrates that either patch condition or the spatial distribution pattern of patches is regulated by the magnitude of shrub encroachment rather than shrub community changes. This

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indicates that the magnitude of encroachment is crucial in regulating changes in ecosystem structure, and therefore needs to be taken into account when making decisions regarding shrub management. Under predicted drier climates, shrub encroachment is likely to intensify, resulting in a more heterogeneous landscape characterized by a shrub community forming a patchwork of fertile islands. Such structural changes will likely alter ecosystem services provided by woody plants, and affect the wellbeing of biotic and abiotic systems.

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Author Contribution Statement

J.D. designed the research. J.D., Y.H., X.G., Y. Y. collected data. J.D., Y.H., Y.W., performed the statistical analyses. J.D. wrote the first draft and W.Z., J.H., D.E. critically revised the manuscript.

Conflict of Interest Statement: The authors declare no competing interests.

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Table 1 Attributes used to assess the 13 soil surface condition (SSC) indices.

No.	**Attribute**	**Interpretation and relevance to soil processes**	**Measurement**
1	Crust resistance	The ability of the soil to resist erosion; qualitative.	The ability of the soil to resist erosion, 1 = non-coherent, 2= easily broken, 3 = moderately hard, 4 = very hard and brittle, 5 = flexible or self-mulching
2	Crust brokenness	The extent to which the soil crust is broken. Broken crusts are more susceptible to erosion. Cracks may be indicative of potential microsites for seeds to settle; qualitative; visual assessment.	The extent to which the soil crust is broken; 0 = no crust, 1 = extensively broken, 2 = moderately broken, 3 = slightly broken, 4 = intact crust
3	Crust stability	The degree to which surface soil aggregates maintain their stability when wetted; qualitative; assessed with the Emerson slake test (Tongway, 1995)	The stability of surface soil aggregates assessed using the Slake Test (Márquez et al., 2004); 0 = not applicable, 1 = very unstable, 2 = unstable, 3 = moderately stable, 4 = very stable
4	Biocrust cover	Cover of biological soil crusts, which protect the soil against erosion, fix nutrients and provide habitat for seeds and soil biota; quantitative, visual assessment.	The cover (%) of biocrusts, including cyanobacteria, fungi, lichens, and mosses
5	Deposited material	Extent and nature of materials deposited on the surface from upslope; quantitative, visual assessment.	The extent of materials deposited on the surface from upslope; 1 = >50%, 2 = 20-50%, 3 = 5-20%, 4 = 0-5%
6	Erosion cover	100 minus the cover of erosional features (e.g. rills, scalds, pedestals); qualitative, visual assessment.	100 minus the cover of erosional features; 1 => 50%, 2 = 20-50%, 3 = 10-25%, 4 =< 10%; percentages present the cover of eroded soil surface
7	Surface roughness	Surface microtopography. Rougher surfaces have a greater ability to retain abiotic and biotic resources; qualitative; visual assessment.	Surface microtopography; 1 = < 3 mm, 2 = 3-8 mm, 3 = 8-25 mm, 4 = large depressions with base, 5 = very large depressions > 100 mm
8	Grazing intensity	The dung of different herbivores. It is used as a proxy of grazing	Counts of dungs

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		activities	
9	Plant basal cover	Indicates examine the effect of cover on overland flow processes. Indicates stability and potential nutrient cycling; quantitative; visual assessment.	The cover (%) of basal area of plants in the microsite
10	Foliage cover	Projected leaf or vegetative material of groundstorey plants (< 1m), which protect soils, sequence carbon and provide habitat for microbes; quantitative, visual assessment.	Plant cover (0-100%)
11	Plant richness	Species richness of groundstorey plants, which are important for soil nutrient processes, the association with microbes and diversity; quantitative, visual assessment.	Species number of plants
12	Litter cover	Indicates the potential for decomposition of plant material and protects the soil against erosion; quantitative; visual assessment.	Litter cover (0-100%)
13	Litter depth	Depth of litter relates to habitat for micro-arthropods and resistance to erosion; quantitative.	Litter depth (mm)

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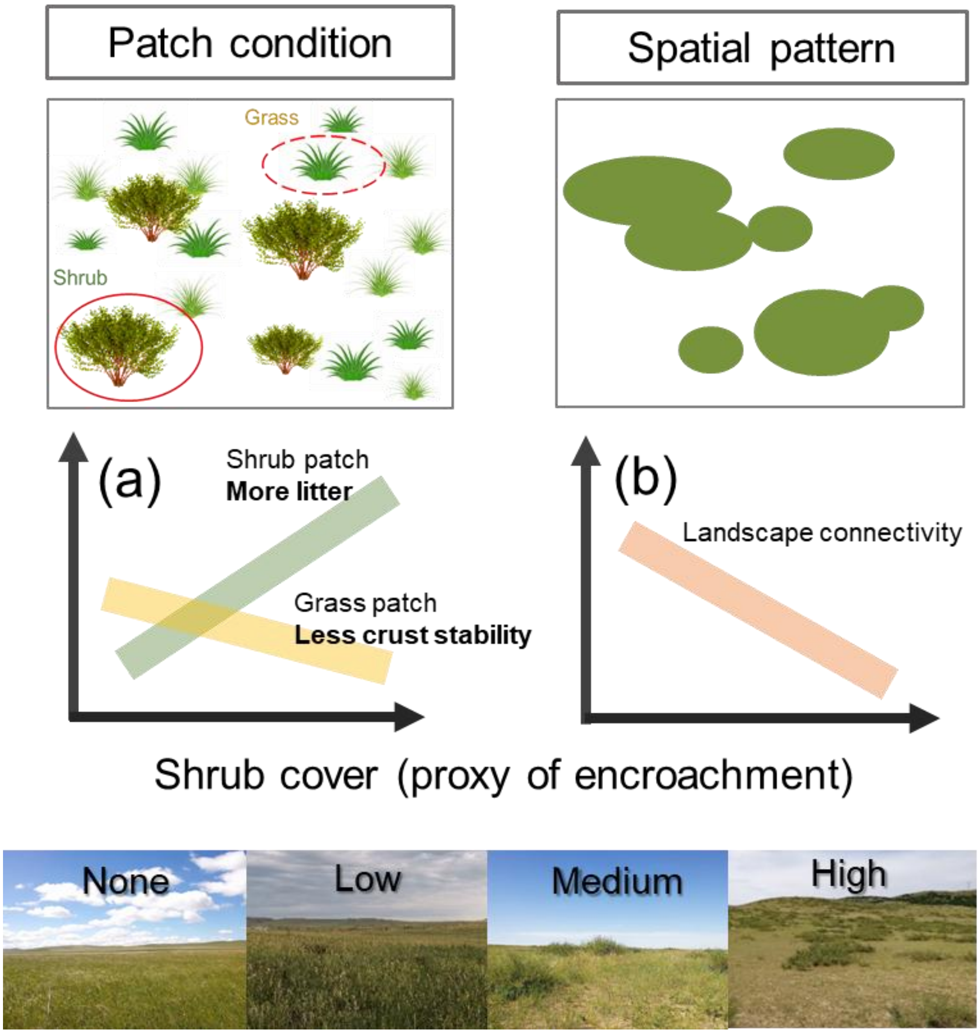
Graphical Abstract



Graphical Abstract

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Figure 1. Hypothetical relationships between the magnitude of shrub encroachment (indicated by shrub cover) and ecosystem structure. (a) ecological condition of patches (e.g., herbaceous biomass beneath patches and soil surface properties), (b) spatial distribution pattern of vegetation patches (e.g., distance between patches, patch brokenness).

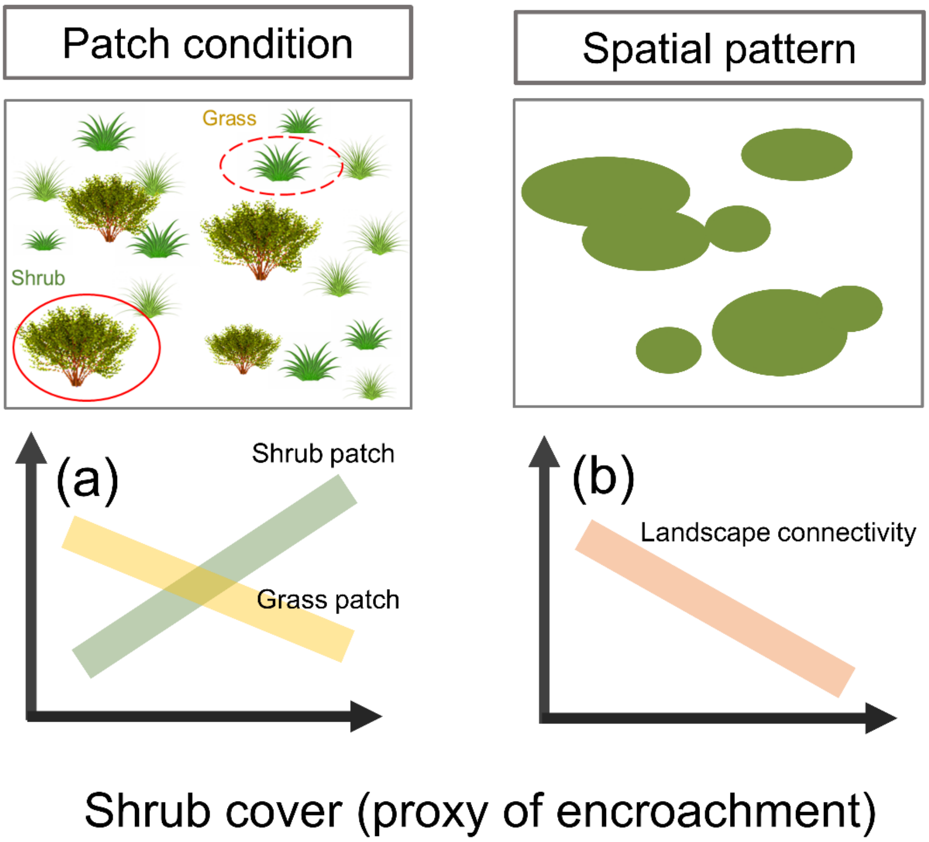

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Figure 2. (a) Sampling sites across Xilingol, Inner Mongolia China and photos of different levels (none, low, medium, high) of encroachment; (b) shrub cover range of sampling sites across the rainfall gradient and (c) the relationship between shrub abundance and shrub cover.

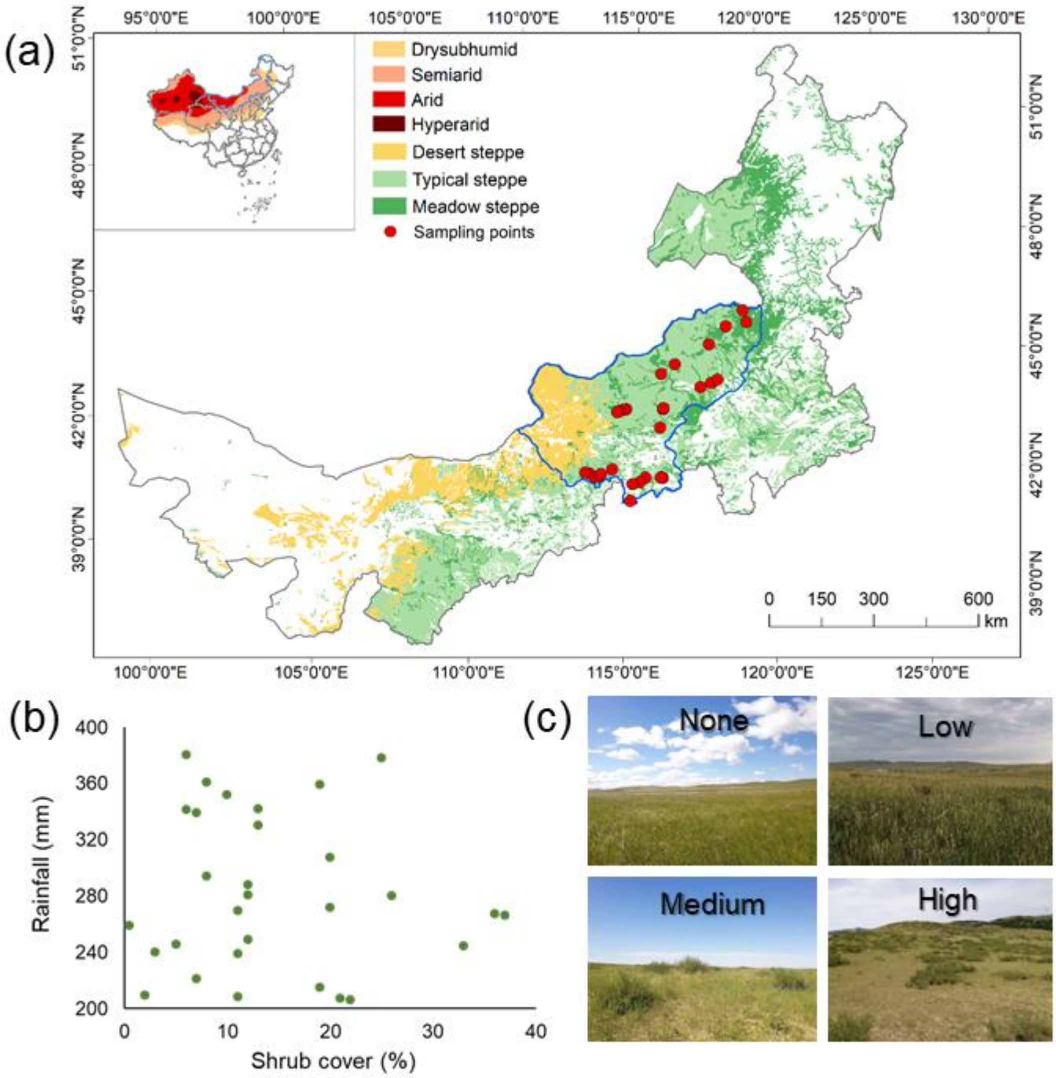

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Figure 3. Variation in shrub community characteristics (the mean, variance, kurtosis and skewness of shrub branch abundance, canopy cover [CD], DBH, shrub height [Ht]) of shrubs along shrub encroachment gradient (square root of shrub cover) and (b) the visualized summary diagram of variation in community characteristics with only significant results showed. * in (a-b) indicate significant (*P*<0.05) linear relationships (Supplementary Table S2).

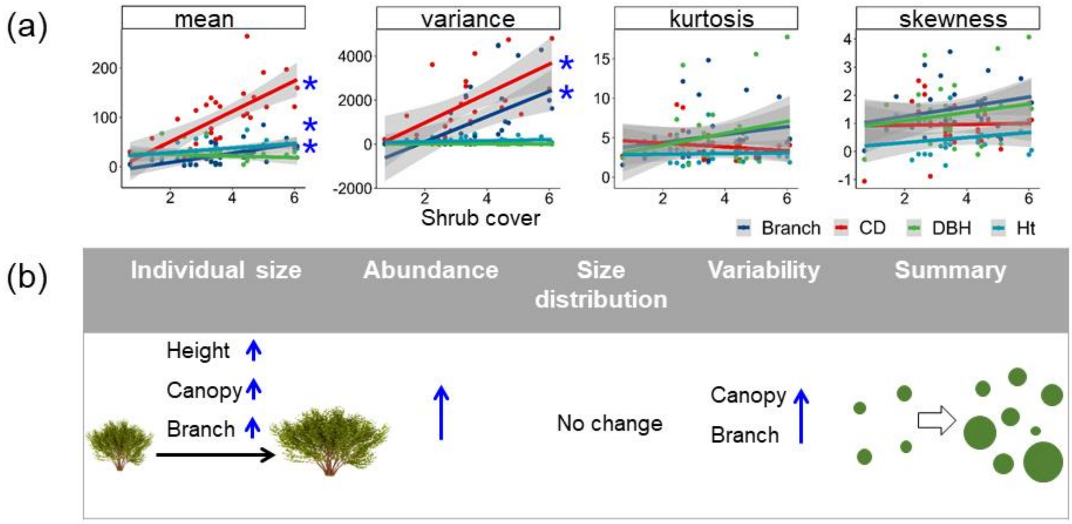

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Figure 4. (a) Difference in patch condition between shrub patches (green) and the interspaced grass patch (yellow), (b) variation of patch condition in shrub patch (green) and the interspaced grass patch (yellow) along shrub encroachment gradient (square root of shrub cover) fitted with linear regression (solid line). * in (a-b) indicate significant (*P*<0.05) linear relationships. Results of linear regression are shown in Supplementary Table S3.

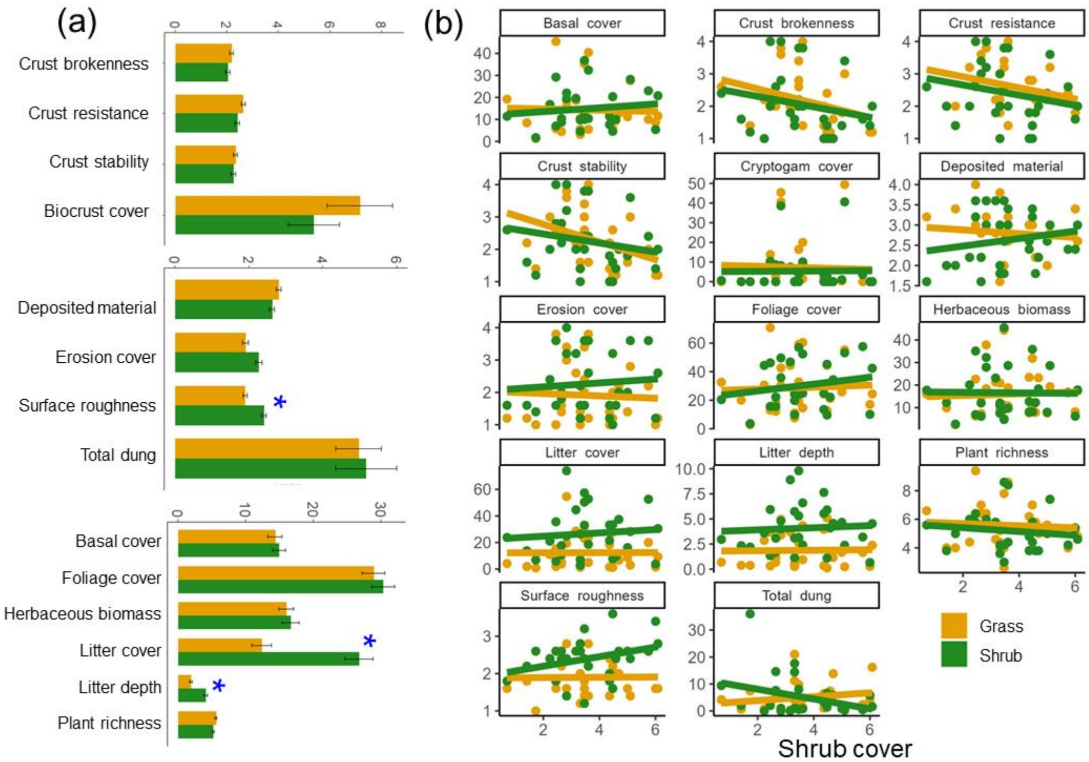

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Figure 5. Variation in the spatial distribution pattern of patches along the gradient in shrub encroachment (square root of shrub cover) fitted with linear regression (solid line) and quantile regression (dot line, 5th, 95th) for vegetation patches (blue) and bare patch (red). AREA SD, Standard Deviation of Patch Area. Results of linear regression are shown in Supplementary Table S4.

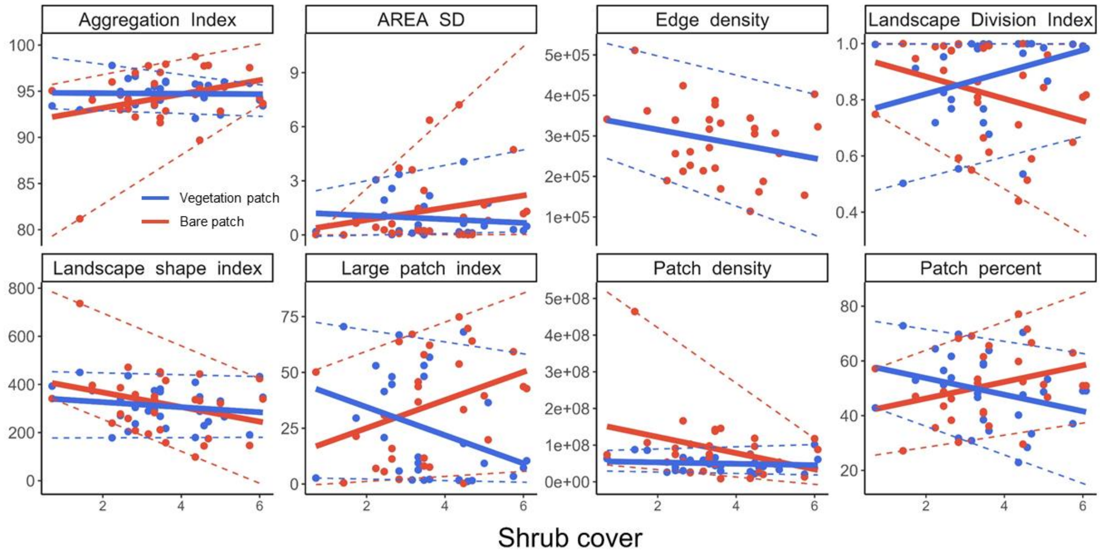

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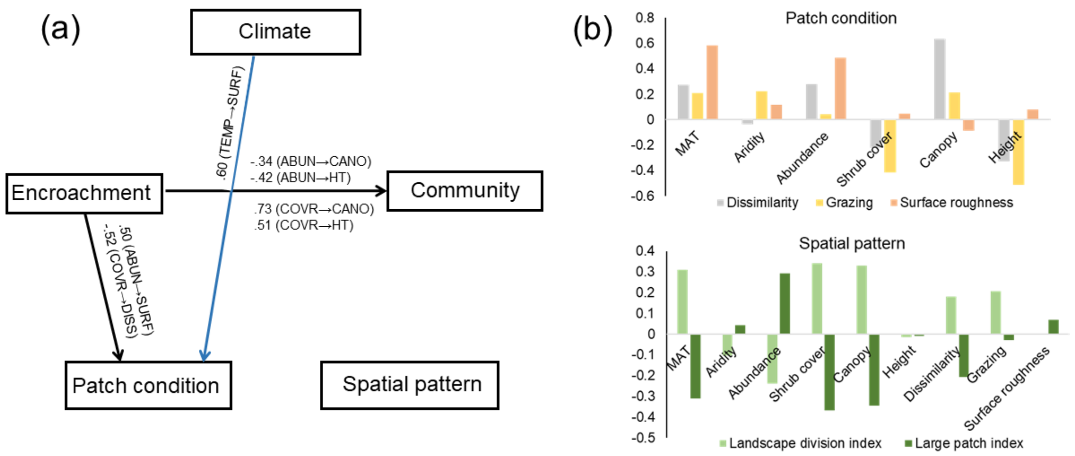
Figure 6. (a) Mechanisms associated with patch condition and spatial distribution pattern of patches, and (b) the standardized total effect. Factors are climate (aridity [AI], mean annual temperature [TEMP]), encroachment magnitude (shrub cover [COVR], shrub abundance [ABUN]), shrub community (shrub height [HT], shrub canopy [CANO]), patch condition (surface roughness of soil under shrubs [SURF], grazing intensity indicated by total livestock dung under shrubs [GRAZ], niche dissimilarity between shrubs and grasses [DISSI]), spatial distribution pattern of patches (large patch index, landscape division index). The detailed *a priori* model structure is shown in Supplementary Fig. S1. Model fit: $\chi^2 = 2.34$, degrees of freedom (df) 10, $P = 0.13$, $R^2 = 0.26$ (patch dissimilarity), 0.39 (grazing), 0.67 (surface roughness), 0.38(large patch index), 0.36 (landscape division index), RMSEA 0.22, N = 30.



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