



Shrub patches capture tumble plants: potential evidence for a self-reinforcing pattern in a semiarid shrub encroached grassland

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Abstract

Background and aims The development of fertile patches within an infertile matrix is a common phenomenon in drylands. Shrub-centered expansion of fertile islands is generally attributed to processes of sediment erosion and deposition, but there have been fewer stud-

ies of how litter might contribute to the development of fertile islands in semiarid shrub grassland.

Methods We quantified the capture of two tumble plant species (*Cleistogenes squarrosa*, *Salsola collina*; also known as tumble weeds) by shrubs across ten sites across 38,000 km² of a semiarid grassland encroached by *Caragana microphylla*.

Results Tumble plants are plants that blow across the grassland propelled by strong winds. Both tumble plant species were found over extensive areas of semiarid grassland, and their distribution coincides with the distribution of *Caragana microphylla*. Biomass production of both tumble plants averaged 12.2 g m⁻² (range: 1.0 to 25.0 g m⁻²) and litter accumulation (amount accruing from wind-blown plants) of both tumble plants was significantly greater beneath shrubs (94.5 ± 28.9 g m⁻² mean ± SE) than in the interspaces (3.3 ± 1.4 g m⁻²). Most of the material collecting under *Caragana microphylla* comprised tumble plants. Increases in the area of *Caragana microphylla* patches did not correspond to greater tumble plant capture. However, the supply of tumble plants was the strongest predictor of capture within shrub hummocks, suggesting that tumble plant capture is source limited rather than sink limited. Our structural equation model indicates that increases in grass cover and height were indirectly and negatively associated with tumble plant capture by reducing the tumble plant supply. Contrary to prediction, shrub height and shrub patch area had no overall effect on the tumble plant capture.

Conclusions Overall, we maintain that the capture of tumble plants by shrubs is an important self-maintaining

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mechanism of shrub-encroached grasslands. Tumble plant abundance is predicted to increase with increasing surface human disturbance and aridity. Therefore, the “shrub-litter island” effect is likely to be an important mechanism for maintaining and promoting the encroachment of shrubs into semiarid grasslands.

Keywords Fertile island · Shrub · Temperate grassland · Tumble plants · Encroachment

Introduction

The formation and development of fertile islands is an important phenomenon in shrub deserts and shrub-encroached grasslands worldwide (Ludwig and Tongway 1995; Okin et al. 2008; Schlesinger et al. 1990, 1996). The creation of shrub-centred fertile islands has been attributed to processes of water and wind erosion, and subsequent deposition, and complex interactions among individual plants and their surrounding soil matrix (Bochet et al. 1999; Cerdà 1997; Puigdefébre and Sanchez 1996; Reid et al. 1999). This redistribution represents a movement of resources (water, seed, soil, organic matter, nutrients) from source areas in the interspaces among shrubs, to the sinks, the elevated areas of soil supporting individual shrubs. These fertile patches are strongly self-reinforcing, as shrub hummocks become resource rich, highly productive patches compared with the source areas (Eldridge et al. 2011), ultimately capturing more resources and increasing in size. While much is known about water and wind as major drivers of fertile island formation in drylands (e.g. Ridolfi et al. 2008; Schlesinger et al. 1990), much of this relates to the abiotic movement of water or soil as causal agents of fertile patchiness. Less well known, however, is the potential role of litter movement (Field et al. 2012; Yan et al. 2016) as a driver of fertile islands, particularly the potential roles of tumble plants.

Wind-blown litter transfer is a common phenomenon worldwide, with important ecological impacts across a range of different landscapes (Fahnestock et al. 2000; Kumada et al. 2009; Schlesinger et al. 1996; Shen et al. 2011). For example, Kumada et al. (2009) showed that the annual physical removal of litter by wind reached 70–82% of the annual litterfall in *Acacia aneura* forests. In the Arctic, wind redistribution of litter from hill and ridge tops to leeward locations during winter leads to the

formation of large patches of accrued litter (Fahnestock et al. 2000). This litter can reduce photosynthetically active radiation and soil temperature, increase the accumulation of carbon (C) and nitrogen (N), and stimulate soil CO₂ efflux at deposition sites throughout the growing season (Fahnestock et al. 2000). In arid and semi-arid shrublands, wind-blown fine soil particles and entrained plant detritus from the shrub interspaces can contribute to the development of fertility islands after deposition under the shrubs (Field et al. 2012; Schlesinger et al. 1996; Yan et al. 2011).

Tumble plants, also known as tumble weeds, are common weedy plants in many drylands. They are characteristically rounded that when detached from the soil, are transported around the landscape, often large distances, until they encounter an obstacle such as a fence or woody plant, against which they accumulate on the windward side (Wang et al. 2002). Tumble plants, which include members of the genus *Salsola*, are widely distributed in natural and agriculture ecosystems worldwide, and part of their extensive global distribution is due to the long-distance dispersal of their seeds (Baker et al. 2008; Borger et al. 2007; Stallings et al. 1995). Anecdotally, these plants are often blamed for damage to fencing, clogging of waterways, or increases in fire hazard due to their habit of accumulating in dense patches (Baker et al. 2008). Wind-blown transport and redistribution of tumble plants are common and ecologically important processes that are affected by differences in topography, meteorological conditions and vegetation pattern (Kumada et al. 2009; Yan et al. 2016).

The accumulation of tumble plants is a common phenomenon in grasslands (Baker et al. 2008; Evans and Young 1972; Shen et al. 2011). Our observations of tumble plants from the semi-arid grassland of Inner Mongolia indicate that they constitute >90% of the biomass of wind-blown litter (Yan, et al. 2016). Previous studies have focused on quantifying the abundance of tumble plants and their morphological adaptations that allow them to disperse long distances by wind (Zhu 1959; Wang et al. 2002). Research in northern China has shown that tumble plants move long distances (Zhu 1959), but the extent of their litter redistribution by wind and the likely ecological impacts have been little studied.

We examined the capture of the tumble plants *Salsola collina* and *Cleistogenes squarrosa* by the shrub *Caragana microphylla* in a semi-arid grassland in Inner Mongolia, to assess the potential magnitude of capture

and the relationship between the shrubs and tumble plants. We had two predictions. First, we expected greater capture of tumble plants around shrubs than in the interspaces. This is because shrubs are much larger than the residual short-stature grasses grazed by livestock that grow in the interspaces. Further, shrubs have thorny stems that likely attach to the tumble plants. If this hypothesis were upheld, we posit that capture of tumble plants might represent a self-reinforcing mechanism for the persistence of *Caragana*-encroached grasslands as shrubs would likely increase in size with the addition of tumble plant-derived organic matter. Second, we expected that the amount of accumulated tumble plants under the shrub canopy will depend on the biomass and composition of tumble plants. If this hypothesis were upheld, this would be strong support for the notion that these shrublands are source- (tumble plant) limited rather than sink- (*Caragana microphylla*) limited.

Methods

Study area

Our study was conducted over an area of about 38,000 km² of semiarid steppe in the Xilingele grasslands in Inner Mongolia, northern China (Fig. 1a). Climate in the area is semiarid, with cold and dry winters, but mild and humid summers, and an annual average rainfall of 270 mm (1981–2014). Precipitation is highly variable, with 75% of the annual total occurring between June and September, and the average daily temperature is −22.3 °C in the coldest month (January) and 18.8 °C in the hottest month (July). Strong winds up to 4.9 ms^{−1} between March and May are capable of transporting large amounts of dust and litter. The dominant plant species found in the natural steppe are *Stipa grandis* P., *Cleistogenes squarrosa* Trin., *Artemisia frigida* Willd., and *Leymus chinensis* Trin. (Yan and Tang, 2008). This area also coincides with the distribution of *Caragana microphylla*, a small N-fixing shrub less than 1 m tall that has encroached into grasslands over the last few decades because of overgrazing and intensified human activities (Zhang et al. 2006). This encroachment of *Caragana microphylla* has created a mosaic of shrub patches resulting from the aggregation of individual shrubs and associated grass-dominated interspaces (Li et al. 2013).

Community-level properties of shrub-encroached grassland

We established ten sites across the study area separated by distances of more than 30 km (Fig. 1a; Supplementary material Table S1). Five plots, 30 m × 30 m, were established at random locations within 3 km of each of the ten sites in order to measure the biomass of tumble plants and other organic material. The distance between any two plots was always >200 m. In August 2017, before plants had been mobilized by wind, we measured tumble plant and grass biomass within three, 1 m × 1 m quadrats randomly placed in the interspaces between shrubs in each plot (total 15 quadrats in each site). Within each quadrat we measured grass cover (by species) using a 50 cm × 50 cm point frame with a grid of 100 crosshairs, and average height of five randomly-chosen grasses. All grasses and tumble plants within the quadrats were removed and separated into species, oven-dried at 65 °C for 48 h, and weighed to determine aboveground biomass. We also randomly established an additional three 30 m × 30 m plots at each site to determine the cover of shrub patches within the grassland. We then marked between six and nine *Caragana microphylla* shrub patches of different size to assess their characteristics (shrub patch area, shrub patch height). These focal shrub patches were then used to calculate the amount of material captured over the next 8 months.

Tumble plant accumulation beneath shrubs

Strong winds can move detached plant material over several kilometres in the semiarid steppe grasslands until an obstacle such as a shrub patch is encountered. Wind-driven movement of tumble plants generally occurs over the non-growing season from early September to mid-May. Therefore, at the end of April 2018, we measured the mass of tumble plants that had accumulated beneath the shrub patches we had marked previously. For each of the six to nine marked shrub patches, we placed a 1 m × 1 m quadrat in the centre of the patch and collected all of the accumulated material. This litter was then separated into different species, dried at 65 °C for 48 h, and weighed to determine litter biomass. Because the newly accumulated litter in the shrub patches comprised mostly tumble plants, including *Cleistogenes squarrosa* and *Salsola collina*, with the new litter that had accumulated from outside the patch occurring on

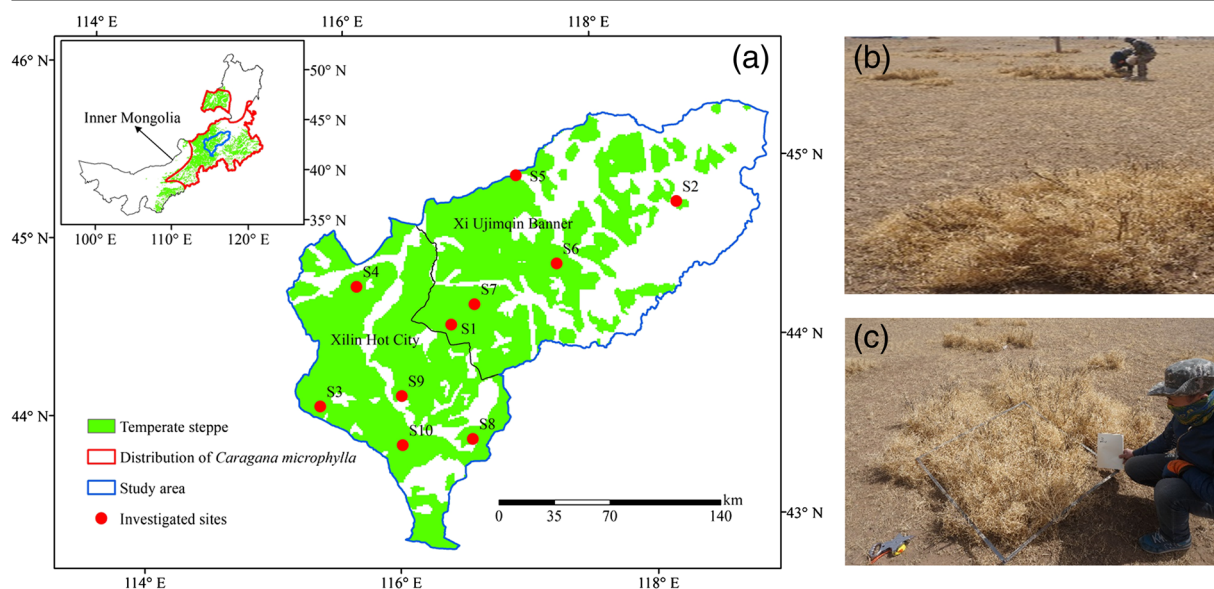


Fig. 1 **a** The location of the study sites and the distribution of *Caragana microphylla* (after Zhao 2005), and accumulation of *Cleistogenes* and *Salsola* within clumps of *Caragana microphylla* (**b**, **c**). Inset is Inner Mongolia

top of the existing litter, new litter and old litter could be clearly distinguished.

Data analyses

We used three steps for the data analyses. First, we assessed the differences in total litter accumulation (sum of *Cleistogenes*, *Salsola* and other litter) between shrub patches and interspaces with a linear model (one-way ANOVA), after averaging data from each of the 10 sites. Data were \log_{10+1} transformed to satisfy assumptions of ANOVA, after testing for normality and homogeneity of variance (Bartlett's test). Separate analyses were then conducted for: 1) *Cleistogenes*, 2) *Salsola*, and 3) other litter. Second, we used linear regression models to test whether biomass of tumble plants increased with increasing shrub patch area or was related to the supply of tumble plants assessed in the interspaces 8 months earlier.

Third, we used Structural Equation Modelling (SEM; Grace 2006) to analyze the effects of shrub patch size and height, and grass cover and height, on the capture of tumble plants after accounting for differences in spatial extent of the sites. Because latitude and longitude were highly positively correlated ($r = 0.96$, $P < 0.001$), we used only longitude in our model. Our a priori model predicted that patch size and tumble plant supply would have strong positive effects on tumble plant capture, but

that increasing grass cover and grass height would have negative effects on capture, potentially by trapping tumble plants in the interspaces. This a priori model was then compared with the variance-covariance matrix to assess an overall goodness-of-fit, using the χ^2 statistic. The goodness of fit test estimates the long-term 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 20 (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 of the shrub-encroached grassland

Shrub patches occupied an average of 25% of the grassland (range: 15 to 37%). The average area of shrub patches was 2.9 m², and the height of the shrub

canopy averaged 26 cm. Grasses occupied 31% of the interspaces with an average height of 5.5 cm, considerably shorter than shrubs (Table 1). Across the 10 sites, the biomass of *Cleistogenes squarrosa* averaged 10.0 g m^{-2} (range: 1.04 to 25.0 g m^{-2}) and *Salsola collina* 2.2 g m^{-2} (range: 0 to 7.4 g m^{-2}) in August 2017, with *Cleistogenes* contributing five-times more litter than *Salsola* (Table S1). Total plant biomass averaged 89.6 g m^{-2} (range: 45.2 to 185.7 g m^{-2} ; Table S1).

Capture of plant material by *Caragana microphylla*

Wind-blown material captured by *Caragana* patches comprised mainly the tumble plants *Cleistogenes squarrosa* and *Salsola collina*, but we also recorded some grasses (*Stipa grandis* and *Leymus chinensis*). We recorded a significantly greater biomass of material within *Caragana* patches than in the interspaces ($F_{1,9} = 110.5$, $P < 0.001$; Fig. 2). When we examined the capture of tumble plant species or grasses separately, we found significantly more *Cleistogenes squarrosa*, *Salsola collina* and grass litter ('other') beneath shrubs than in the interspaces ($P < 0.001$; Fig. 2). Together, the two tumble plant species made up about 14% of total biomass across the 10 sites (Table S1). We found that the capture of tumble plants by *Caragana* increased with increases in the supply of plants at the community level (Fig. 3) but increases in patch area did not correspond with greater capture. Overall, *Caragana* captured 65% more *Cleistogenes* than *Salsola* for a given biomass of tumble plants.

Our structural equation modelling showed that the supply of tumble plants was the strongest predictor of capture within shrub hummocks. Contrary to prediction, shrub height and shrub patch area had no overall effect on the tumble plant capture. Increases in grass cover and height, and increased longitude had overall suppressive effects on tumble plant capture, indirectly, by reducing the supply of tumble plants (Fig. 3).

Discussion

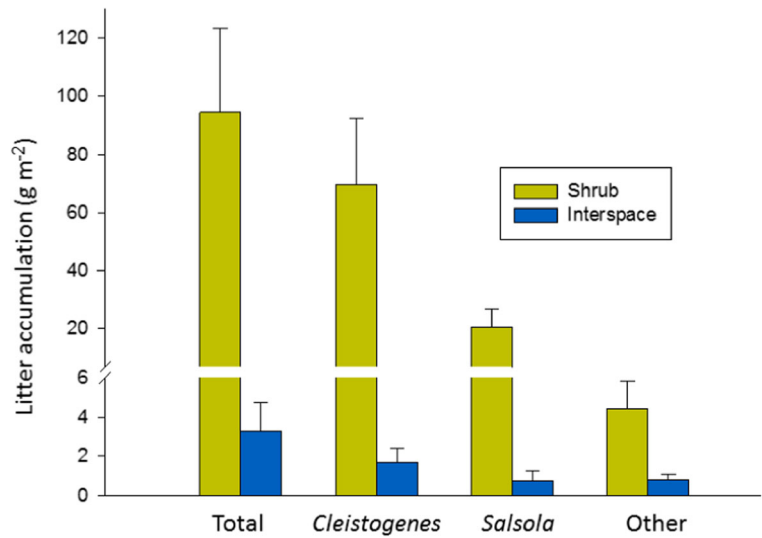
Our study showed that about thirty-times more tumble plant litter accumulated beneath shrub patches than in the grassland interspaces (Fig. 2), supporting our first prediction, and providing empirical evidence that the capture of tumble plants is a significant phenomenon in *Caragana* shrublands. Three potential mechanisms underpin the phenomenon of resource capture in *Caragana* shrublands. First, both source (tumble plants) and sink (*Caragana microphylla*) increase in response to increasing overgrazing and climate change so that increases in potential sinks coincide with increases in source material. Encroachment of *Caragana microphylla* into grasslands is a widespread phenomenon in the temperate steppe on the Mongolian Plateau (Wang et al. 2002), largely due to increasing disturbance by grazing and changes in warming and drying cycles across the region over the past few decades (Peng et al. 2013; Li et al. 2013). Our source plant *Cleistogenes squarrosa* is a perennial xeromorphic bunchgrass that usually appears as an associated subdominant species in temperate steppe, but dominates under overgrazing (Wang et al. 2002), particularly in areas where wind erosion has increased the deposition of coarse material (Yan et al. 2011). Similarly, *Salsola collina* is an annual plant widely distributed in the temperate steppe, which increases in abundance with overgrazing (Wang et al. 2002). Like many *Salsola* spp. globally, it has a short life cycle, is a prolific seeder (> 7500 seeds per plant in *Salsola australis*; Borger et al. 2007), and is a strong invader (Borger et al. 2007). Thus, both our source and sink species respond similarly to different environmental conditions, and co-occur across the same biogeographical region.

Second, the morphology of tumble plants and the structure of *Caragana* patches provide the necessary mechanism for the capture process. *Caragana microphylla* plants are generally 40–70 cm tall, have

Table 1 Plant community properties of shrub-encroached grasslands in the study area in April 2018

Attribute	n	Mean	SE	Minimum	Maximum
Community-level shrub patch cover (%)	30	25.2	2.5	15.0	37.0
Shrub patch area (m^2)	86	2.9	0.5	0.7	30.4
Shrub patch height (cm)	86	26.6	1.0	11.7	50.3
Interspace grass cover (%)	86	30.7	3.6	9.0	80.0
Interspace grass height (cm)	86	5.5	0.4	1.8	10.3

Fig. 2 Mean (\pm SE) mass of organic matter accumulating under canopy of *Caragana microphylla* shrubs and interspace for four different litter components. In all cases there was significantly more organic matter trapped under shrubs than in the interspaces at $P < 0.05$



branches with short spines, and occur in patches up to 10 m across, depending on the level of development. Large shrub patches such as these, which nestle within a grassland mosaic, have been shown to alter microclimates by reducing wind speeds (D'Odorico et al. 2013; Field et al. 2012). The shrub patches can also increase

the deposition of sediment and have an interception effect on windblown organic material. Added to this is the fact that our source plants *Cleistogenes squarrosa* and *Salsola collina* are both typical tumble plant species. Specifically, after the seeds of *Cleistogenes squarrosa* mature, the seed-bearing branches curl

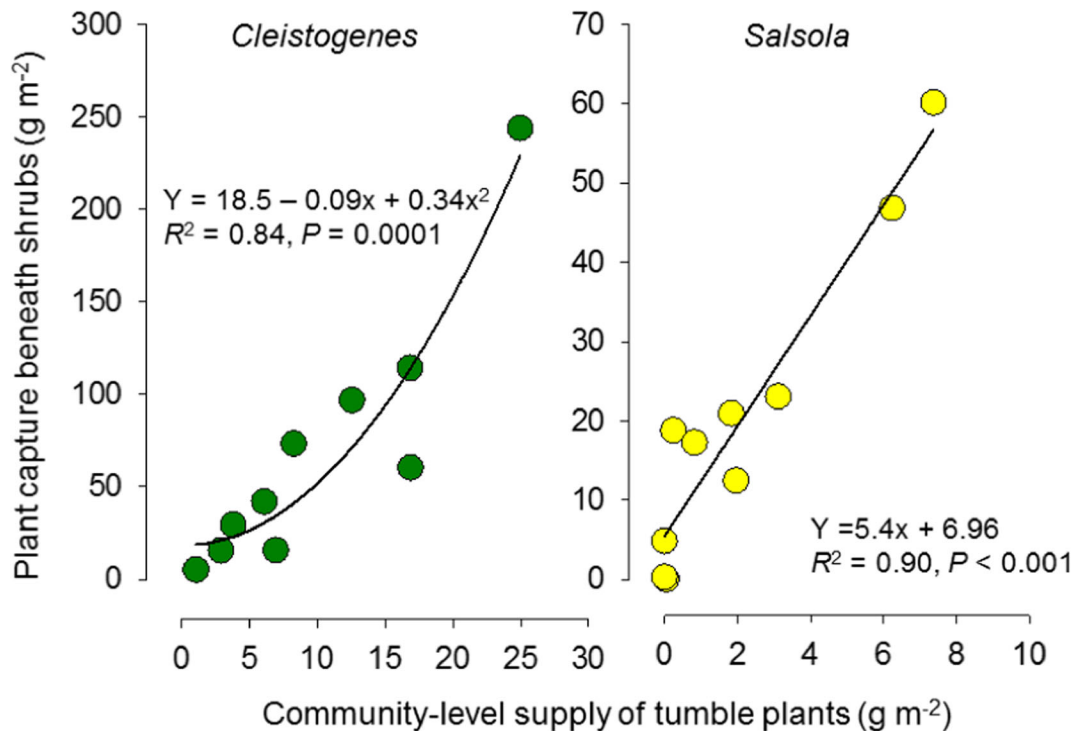


Fig. 3 Relationships between the supply of tumble plants at the community scale at the beginning of the season and the capture of plants beneath the canopies of *Caragana microphylla* at the end of the growing season for *Cleistogenes* and *Salsola* separately

inwards from the top of the inflorescences, the plants rapidly desiccate, and the whole plant becomes lighter, forming a small spherical shape (generally below 10 cm diameter). The leaves on the seed-bearing branches shrink, and the wind-bearing surface increases. Then, the base of the seed-bearing branches break free and the detached plant tumbles with the wind across the vast grassland (Wang et al. 2002). Unlike small and light *Cleistogenes squarrosa*, *Salsola collina* has a large crown, up to 1 m across (Tai et al. 2001), but is shallow rooted, so that the crowns also readily detach upon senescence (Wang et al. 2002), causing the above-ground part of the plant to tumble across the grassland propelled by strong winds. Thus, both the sink and source plants in our study have features such as spiny tips and dense spine-like clusters or curled seed-bearing branches, ensuring that plants coming into contact are very difficult to detach. Third, strong winds during the non-growing season in the temperate steppe provide sufficient driving force to mobilise long-distance dispersal of tumble plants. The threshold wind velocity required to mobilise *Cleistogenes squarrosa* in the non-growing season (October to April) is 0.7 m s^{-1} ; substantially less than the average wind speed of 4 m s^{-1} during that period (Yan et al. 2016).

A larger shrub patch should imply a greater capture of resources (sensu self-organisational theory (Rietkerk and van de Koppel 2008), but this did not occur in our study. Our structural equation model revealed no significant relationship between litter capture and either shrub patch size or height (Fig. 4). One potential explanation is that our system is source limited not sink limited, which is consistent with our result that capture was related most strongly to the supply of tumble plants (Figs. 3 and 4) and consistent with the second prediction. Thus, the sink capacity of our system is unsaturated, which could be due to a relatively greater landscape-level coverage of shrub hummocks and/or a lower biomass of tumble plants. Tumble plants are weeds of agricultural systems, particularly summer fallows, and require regular disturbance to maintain their populations (Borger et al. 2007). The abundance of our tumble plants is likely to decline as land managers move more towards sustainable grazing and away from cropping (Wali 1999).

Ecological theory suggests that the accumulation of resources in drylands should lead to changes in ecosystem functions and changes in the spatial scale at which resources are distributed (Maestre et al. 2009; Schlesinger et al. 1990, 1996). Consistent with source-

sink relationships in deserts, the accumulation of tumble plants beneath shrubs would increase the organic matter and nutrient inputs into the shrub patches (Eldridge et al. 2011; Vetaas 1992). Although we have no data on litter decomposition from beneath the shrub canopy in our study, the decomposition characteristics of different plant species within grasslands is available from previous studies (Table S2). Published studies (Yin et al. 1994; Wang 2018) show that 95% decomposition of *Cleistogenes squarrosa* and *Salsola collina* litter is achieved in 5.2 and 8.9 years, respectively. Decomposition of litter beneath the shrub canopies would be expected to be faster than in the grass community due to the generally greater levels of soil moisture and microbial activity beneath shrubs (Li et al. 2013). Organic carbon (OC) and, total nitrogen (TN) contents of the litter of the two tumble plants ranged from 41.0 to 54.3%, and 1.7 to 2.0%, respectively (Table S2, Dan et al. 2015; Wang 2018), which equates to annual additions of 45.4 and 1.7 g m^{-2} of OC and TN, respectively. Based on the decomposition rates reported above, this OC and TN would accrue within the soil over a period of about 5 to 9 years (Table S2) based on 95% decomposition. Thus, old and new litter would coexist beneath the shrub canopy due to the relatively slow rate of complete decomposition. A previous study (Yan et al. 2016) showed that the biomass of old litter closer to the soil surface was almost double (1.8 times) that of new litter deposited in the upper layer. Therefore, the inputs of C and N to the shrub patches will be enhanced over time due to multi-year accumulation of wind-blown litter and its decomposition. Previous studies in the Mongolian grasslands (Li et al. 2016) have demonstrated that soil organic C and N values are significantly greater under shrubs than in the interspace. Thus, the capture of a large amount of tumble plant litter potentially results in the formation of “shrub-litter island” (Travers and Eldridge 2015), which will further reinforce the “fertile island” effect already apparent under the canopies of the N-fixing *Caragana* shrubs (Ludwig and Tongway 1995).

Our observations indicate that the addition of tumble plants to the shrub matrix increases the size and density of the shrub patches, with a potentially greater effect on microclimate. Denser vegetation patches moderate temperatures by cooling the soil surface during the warm season and warming it in the cold season (D’Odorico et al. 2010; He et al. 2015; Li et al. 2013; Schlesinger and Pilmanis 1998; Yan et al. 2018). Denser patches also increase the capture of wind-blown sediments by

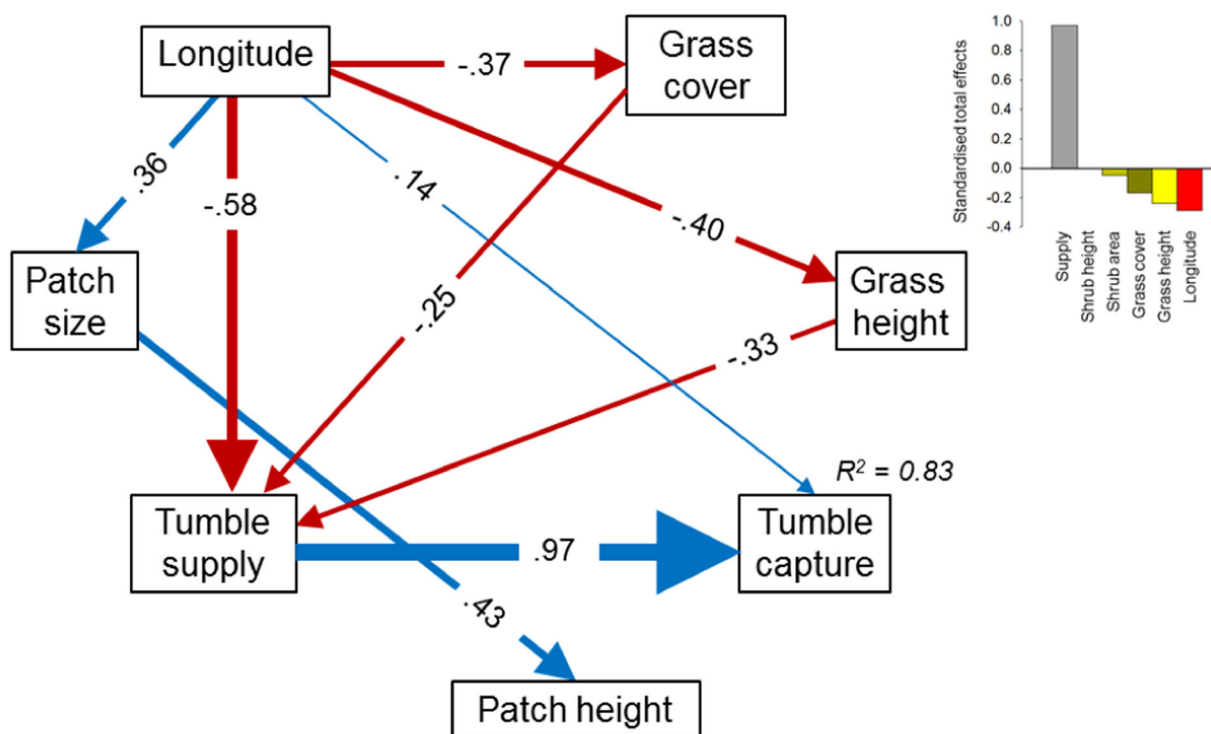


Fig. 4 Structural equation model depicting the effects of shrub patch size and height, grass cover and height, latitude and tumble plant (*Cleistogenes* + *Salsola*) supply on the capture of tumble plants. The width of arrows is proportional to the path coefficient, with continuous blue (positive) and red (negative) lines indicating the sign of the relationships. The strength of the path coefficient is presented on each pathway. Non-significant pathways have been

omitted for clarity. The proportion of variance explained (R^2) appears above tumble capture in the model. Inset is the standardized total effects, the sum of all direct and indirect effects of tumble plant supply, shrub patch size and height, grass cover and height on tumble plant capture. $\chi^2 = 2.35$, $df = 4$, $P = 0.67$, GFI = 0.992, RMSEA = 0.00, Bollen-Stine = 0.51

increasing the threshold velocity at which particles are maintained in the airstream (Leenders et al. 2011). Furthermore, these vegetation patches can also capture and intercept wind-blown snow, providing a subnival cavity that increases the temperature under the thick snow in winter. This reduces plant mortality due to low temperatures, and increases soil water content the following spring, protecting the plants against drought in the early growing season (Wang et al. 2002) (Fig. 5). Many studies have reported that there have been significant increases in the abundance of both *Cleistogenes squarrosa* and *Caragana microphylla* in the temperate steppe in Inner Mongolia in recent decades (Zhang et al. 2006; Li et al. 2013), which is attributed generally to increasing disturbances such as grazing (Peng et al. 2013). Our study provides additional evidence that the positive feedback effect of disturbance-induced capture of plant material may facilitate the spread and development of both plant species during the grassland degradation process.

In summary, the capture of tumble plant litter by shrubs is an important process in shrub-encroached grasslands that is driven by human disturbance (grazing) and climate change. *Caragana microphylla*, a deep-rooted native shrub, can access water deep in the profile, making it largely resistant to increasing aridity, and the short spines on its branches act to reduce herbivory by livestock, giving it a competitive advantage over grasses and forbs in a drier, grazed environment (Peng et al. 2013). Overgrazing might result in a more aggregated distribution of *Caragana* as it forms larger patches (Fig. 5, T1), which coincides with an increase in tumble plants abundance, which is also driven by overgrazing (Wang et al. 2002). Wind, increasing size of shrub patches and more abundant tumble plants promote the development of “shrub-litter islands” (Fig. 2; Fig. 5, T2), resulting in a self-reinforcing mechanism that promotes the shrub persistence (Fig. 5, T3), analogous to the development of shrub islands elsewhere (e.g. western USA; He et al. 2015; Schlesinger et al. 1990).

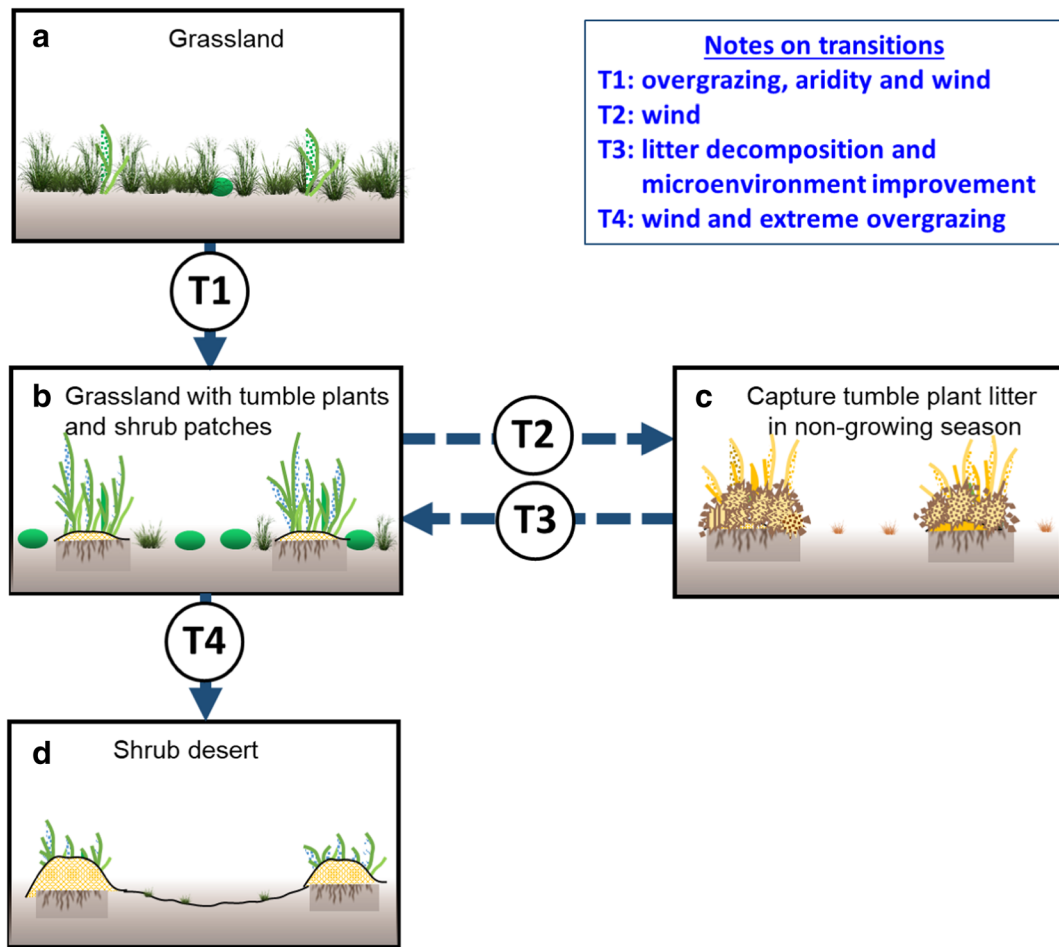


Fig. 5 State-and-Transition model of shrub-grass dynamics for *Caragana microphylla* driven by overgrazing, aridity and wind. A, B and D represent three states of shrub grassland driven by

overgrazing, aridity and wind, C represent a special non-growing season state with an obvious “shrub-litter island” effect with transitions to state B via T2

The only difference is that, in the case of *Caragana*, the mechanism involves more obvious movement of plant biomass, as well as other possible factors such as sediment and water (Jin et al. 2009; Shen et al. 2011; Jin et al. 2013). At a given regime of grazing-induced disturbance, grassland with shrub patches and tumble plants might result in a stable system due to the “shrub-litter island” effect. However, continued and prolonged extreme overgrazing coupled with wind, will likely further deplete palatable grasses and associated tumble plants, resulting in more exposed soils (Fig. 5, T4). Thus, the “shrub-litter island” effect is likely to be an important mechanism of ecosystem self-organization or self-resistance to sustain stable and productive grassland-shrubland mosaics under a regime of increased human activity as we move into a drier world.

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