The Spatial Pattern and Interactions of Woody Plants on the Temperate Savanna of Inner Mongolia, China: The Effects of Alternating Seasonal Grazing-Mowing Regimes

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Abstract

Ulmus pumila tree-dominated temperate savanna, which is distributed widely throughout the forest-steppe ecotone on the Mongolian Plateau, is a relatively stable woody-herbaceous complex ecosystem in northern China. Relatively more attention has been paid to the degradation of typical steppe areas, whereas less focus has been placed on the succession of this typical temperate savanna under the present management regime. In this study, we established 3 sample plots 100 m×100 m in size along a gradient of fixed distances from one herd-e r's stationary site and then surveyed all the woody plants in these plots. A spatial point pattern analysis was employed to clarify the spatial distribution and interaction of these woody plants. The results indicated that old Ulmus pumila trees (DBH/ C21 cm) showed a random distribution and that medium Ulmus pumila trees (5 cm/DBH < 20 cm) showed an aggregated distribution at a smaller scale and a random distribution at a larger scale; few or no juvenile trees (DBH/ < 5 cm) were present, and seedlings (without DBH) formed aggregations in all 3 plots. These findings can be explained by an alternate seasonal grazing-mowing regime (exclosure in summer, mowing in autumn and grazing in winter and spring); the shrubs in all 3 plots exist along a grazing gradient that harbors xerophytic and mesophytic shrubs. Of these shrubs, xerophytic shrubs show significant aggregation at a smaller scale (0-5.5 m), whereas mesophytic shrubs show significant aggregation at a larger scale (0-25 m), which may be the result of the dual effects of grazing pressure and climate change. Medium trees and seedlings significantly facilitate the distributions of xerophytic shrubs and compete significantly with mesophytic shrubs due to differences in water use strategies. We conclude that the implementation of an alternative grazing-mowing regime results in xerophytic shrub encroachment or existence, breaking the chain of normal succession in a Ulmus pumila tree community in this typical temperate savanna ecosystem. This might eventually result in the degradation of the original tree-dominated savanna to a xerophytic shrub-dominated savanna.
Introduction

In the early 1980s, the Livestock and Rangeland Double-Contract Responsibility System (LRDCRS) was implemented in the pastoral regions of Northern China, with strong expectations of increasing livestock productivity and rehabilitating degraded rangeland [1, 2]. This measure was followed by the establishment of fixed and exclusive resource boundaries and the adoption of alternating seasonal grazing (winter and spring) and mowing (autumn) regimes as a commonly accepted management tool [1, 3]. However, some research shows that rangeland degradation was never halted [4–7]. This continued degradation has been attributed to climatic change, such as long-term and high frequent drought, or human activities, such as overgrazing and overexploitation [8–10]. Shrub encroachment into grassland has also been considered an obvious indicator of rangeland degradation in the pastoral regions of northern China [11, 12].

As a common tree species distributed widely throughout the forest-steppe ecotone on the Mongolian Plateau [13, 14], in association with grasses, *Ulmus pumila* trees form a stable savanna-like woody-herbaceous complex ecosystem in the Horqin Sandy Land, the Otindag Sandy Land and the Hulunbeier Sandy Land of northern China [15, 16]. Sparse *U. pumila* trees within the savanna have ecological significance in sand stabilization and small-habitat provision for livestock [17]. However, although it represents an important consideration for the steppe in this region, the degradation of this temperate savanna, especially the sparse *U. pumila* tree pattern in recent years, has attracted little attention from the public or scientists [18, 19]. A small number of studies have shown that, compared with other species, *U. pumila* has faced a major regeneration challenge [20–23]. *U. pumila* seedlings often suffer from severe water stress during dry summers is caused by repeated cycles of drying in the upper soil layers [24, 25]. Wang et al. [22] noted that more than 90% of the current-year seedlings in fenced plots died because of their vulnerability to drought. Jiang et al. [23] discussed the effect of vegetation cover on the recruitment of *U. pumila*, finding that the highest initial seed density was found under the highest vegetation cover.

Spatial pattern analysis is an important method for studying the interactions and relationships among different plant populations and their environments [26, 27]. The analysis of a species’ spatial pattern will help us to understand both the ecological process that forms the pattern (such as seed dispersal, intra- and inter-specific competition, interference, and environmental heterogeneity) and the ecophysiological traits of the plant species, including the relationship between these plants and the environment [28–30]. The spatial pattern of species and the spatial correlation between species have a significant impact on growth, reproduction, death, resource utilization and gap formation among species [29, 31]. Recently, a spatial pattern analysis method has been used for clarifying the vegetation degradation processes underlying the individual pattern in semi-arid and arid areas [32–35].

In this study, we selected 3 fixed sample plots 100 m×100 m in size along a predetermined grazing gradient (distance from the herder’s stationary site), and the spatial pattern of the individual woody plants (including *U. pumila* trees and shrubs) and interactions among these woody plants were analyzed using the spatial point pattern method. Two key points are discussed: (1) whether an alternating seasonal grazing-mowing regime affects the pattern of elm trees and shrub occurrence or presence, and (2) whether alternating seasonal grazing-mowing management reduces recruitment of the *U. pumila* trees. This study will be helpful for a better understanding of the degradation processes affecting a *U. pumila*-dominated savanna.
Materials and Methods

Ethics Statement

The study site is located in the Otindag Sandy Land. It is administered by the Sanggendalai township of the Xilinguole League, Inner Mongolia (115°16'E, 42°50'N). The study was conducted on private land. We paid the owner of the land for permission to conduct the study on this site. No rare or endangered wild animals or plants were collected in this experiment. Permit restrictions also required the experiment to be conducted without the use of open flame to prevent forest fires and without the cutting of tall trees to protect the forest ecosystem from damage. In addition, the samples consisted of common tree species and shrubs, so sampling had no direct impact on vertebrate survival. This experiment did not use wild animals or plants as research objects and did not pose a threat to the environment.

Study site

The study site is located in the Otindag Sandy Land (Fig 1). It is administered by the Sanggendalai township of the Xilinguole League, Inner Mongolia (115°16'E, 42°50'N). The elevation is approximately 1320 m. The local climate is continental, with hot summers, long and cold winters, and a mean annual precipitation of 250–350 mm, more than 70% of which occurs from June to August. The annual mean temperature is 1.7°C, the extreme minimum temperature is -38°C, and the annual accumulated temperature (≥10°C) is 2000°C. The frostless period is approximately 105 days, the annual sunshine duration is greater than 1000 h, the annual mean wind speed is 4 m/s, and the wind level exceeding a Beaufort scale value of 8 is 90 days per year. The main soil types are aeolian sandy soil with a mean depth of 200 cm and a calcic horizon occurring at a depth of 30–100 cm. This horizon is extremely hard and does not allow plant roots to penetrate it.

The local herders currently select alternating seasonal grazing (winter and spring) and mowing (autumn) regimes, whereas annual grazing was previously implemented. The area’s grazing livestock are primarily cattle. To prevent grassland degradation, grazing is prohibited during the growing season of the grasses (summer), and the herders mow grass to reserve food for animals in winter. Both grazing and mowing occur every year. No fire has happened in this study site.

Study species

Trees. *U. pumila*: This tree can survive to an age of more than 40 years. The species can grow to a height of more than 10 m. *U. pumila* seeds are wind-dispersed and can be dispersed to a great distance from their parents during the windy season.

Shrubs. Xerophytic shrubs: *Caragana microphylla* Lam is a long-lived shrub with multiple stems bearing thorns and compound leaves. Flowering occurs in May and lasts approximately 20 days. Seeds ripen in July, and seed germination is triggered by summer rainfall. Shoots usually grow out at the end of the flowering period. *Spiraea aquilegifolia* Pall is a long-lived shrub. Flowering occurs in May-July, and seeding occurs in August-September; *Ribes diacanthum* is a long-lived shrub. Flowering occurs in May-June, and seeding occurs in July-August; *Salix lineartipularis* is a long lived shrub.

Mesophytic shrubs: *Betula fruticosa* Pall is a long-lived shrub. Seeds are dispersed by animals.

Data collection

A fenced rangeland tract (approximately 50 ha), typical of *U. pumila*-dominated savanna and contracted by a herder family, was selected as the study site. The site was placed under alternative seasonal grazing and mowing management in approximately the year 2000. Seasonal
grazing occurred in the winter and spring, and mowing was implemented in autumn with a small tractor mower. In August of 2014, 3 sample plots 100 m×100 m in size were established at fixed distances from the herder’s stationary site (numbered as plot 1, plot 2 and plot 3 from near to far). Plot 1 was 1 km distant from the herder’s stationary site, plot 2 was 2 km distant, and plot 3 was 3 km distant. All the 3 plots have basically identical natural conditions (such as soil types, geomorphology, rainfall). Each plot (100 m × 100 m) was divided into 400 contiguous 5 m × 5 m plots, and the name, diameter (DBH or collar diameter), height and spatial coordinates of all the woody plants (trees and shrubs) were recorded in each plot. All individual woody plants in the three plots were mapped using a total station transit (model GTS-3B, Topcon, Paramus, New Jersey, USA) with an accuracy of approximately 1 cm.

All the U. pumila trees were classified into 4 categories according to their DBH, namely, old adult trees (DBH ≥ 20 cm), medium adult trees (5 cm ≤ DBH < 20 cm), juvenile trees (DBH < 5 cm) and seedlings (without DBH), a classification that is consistent with previous research results [36]. Shrubs were also classified into two categories according to their ecophysiological traits[37], namely, xerophytes, including Caragana microphylla Lam, Spiraea aquilegfolia Pall, Ribes diacanthum and Salix linearitipularis, and mesophytes, including Betula fruticosa Pall. (Table 1; Fig 2). As few individuals in the juvenile tree category were found, this category was not included in the spatial pattern analysis.

Data analysis

Ripley’s K-function and the pair-correlation g-function are common techniques for univariate and bivariate point-pattern analysis. The function K(r) is the expected number of points in a circle of radius r centered at an arbitrary point (which is not counted), divided by the intensity λ of the pattern.

The alternative pair correlation function g(r), which arises if the circles of Ripley’s K-function are replaced by rings, gives the expected number of points at distance r from an arbitrary point, divided by the intensity λ of the pattern. The function g(r) has the additional advantage that it is a probability density function with the interpretation of a neighborhood density, which is more intuitive than an accumulative measure[38]. Therefore, the pair-correlation function g(r) is
especially sensitive to small-scale effects. In this study, we used univariate and bivariate pair correlation functions \(g(r)\) and \(g_{12}(r)\) to quantify the spatial pattern of individual woody plants and interactions among them. For univariate analysis, the formula used\[^{31, 39–41}\] is as follows:

\[
g(t) = \frac{A^2}{2 \pi t} \sum_{i=1}^{n} \sum_{j \neq i}^{n} w_{ij} k_h(t - |x_i - x_j|),
\]

where \(A\) is the plot area, \(n\) is the total number of plants and \(w_{ij}\) is a weighting factor correcting for edge effects. \(k_h\) is a kernel function, which is a weighting function applying maximum weight to point pairs with a distance exactly equal to \(t\) but incorporating point pairs at an approximate distance \(t\) with reduced weight. This weight falls to zero if the actual distance between the points differs from \(t\) more than \(h\), the so-called bandwidth parameter. At a given distance \(r\), values of \(g(r) > 1\) indicate that interpoint distances around \(r\) are relatively more frequent than they would be under complete spatial randomness (CSR). If this is the case for small values of \(r\), there is typically clustering. Conversely, values of \(g(r) < 1\) indicate that interpoint distances around \(r\) are relatively less frequent than they would be under CSR. If this is the case for small values of \(r\), the pattern shows regularity.

For bivariate analysis, the formula used\[^{39–41}\] is as follows:

\[
g_{12}(t) = \frac{A^2}{2 \pi t n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij} k_h(t - |x_i - y_j|),
\]

where \(x_i, i=1, \ldots, n_1\), and \(y_j, j=1, \ldots, n_2\) are the points of groups 1 and 2, respectively, with the same weights \(w_{ij}\) and kernel function \(k_h\) as above. At a given distance \(r\), values of \(g_{12}(r) > 1\) indicate that species 2 is positively associated with species 1 at distance \(r\). Values of \(g_{12}(r) = 1\) indicate that there is no interaction between species 1 and 2. Values of \(g_{12}(r) < 1\) indicate that species 2 is negatively associated with species 1.

The keys for successful application of the \(g\) function are the selection of an appropriate null model that responds to the specific biological question asked and the correct interpretation of a given departure of data from the null model\[^{40}\]. In this study, we used the null model of complete spatial randomness (CSR) as a null hypothesis for the univariate analyses of three tree

### Table 1. Classification of *U. pumila* trees and shrubs and their basic parameters.

| species            | Category* | Plot 1 | Plot 2 | Plot 3 |
|--------------------|-----------|--------|--------|--------|
|                    | \(N\)     | \(H\)  | \(N\)  | \(H\)  |
| *U. pumila* trees  | Old       | 40     | 7.4±0.94 | 63     | 7.3±1.53 |
|                    | Medium    | 50     | 5.3±0.93 | 85     | 5.1±1.27 |
|                    | Juvenile  | 2      | 1.7±0.30 | 2      | 2.4±0.22 |
|                    | Seedling  | 53     | 0.23±0.16 | 108    | 0.28±0.22 |
| xerophytic shrubs  | CaraMicr  | 58     | 0.41±0.13 | 27     | 0.39±0.10 |
|                    | SpirAqui  | 215    | 0.42±0.17 | 158    | 0.41±0.15 |
|                    | RibeDiac  | \(\_\) | \(\_\)   | 12     | 0.31±0.10 |
|                    | SaliLine  | \(\_\) | \(\_\)   | 17     | 2.0±0.21  |
| mesophytic shrubs  | BetuFrut  | \(\_\) | \(\_\)   | 46     | 2.2±0.35  |

* Latin name abbreviations: CaraMicr- *Caragana microphylla* Lam., SpirAqui- *Spiraea aquilegifolia* Pall, RibeDiac- *Ribes diacanthum*, SaliLine- *Salix linearitipularis*, BetuFrut- *Betula fruticosa* Pall.
categories (old trees, medium trees and seedlings), and for two shrub categories (xerophytes, mesophytes).

For the bivariate analyses, two cases were considered. In the first case, the relationship between small and large trees was considered. Because large trees may impact the distribution pattern of small trees within their area of influence (competition), we conducted a bivariate g function analysis for these two size classes using both the toroidal shift and the antecedent condition null model options [40]. This tests whether the patterns of distribution of small and large trees were generated by independent processes. The antecedent condition model tests whether one pattern (small trees) is influenced by a second pattern (large trees), assessing whether there are more (or fewer) small trees in the neighborhood of large trees than expected under a random distribution of small trees [39]. The second case concerns the interaction between trees and shrubs. Because the spatial distributions of plants in plots seem to be affected significantly by drought stress and habitat heterogeneity (e.g., soil patch and microtopography), we examined the spatial association between the two species with the independent null model [40].

To assess the significance of the test function under the null model, we generated an approximate (two-sided) 95% simulation envelope by calculating for each distance r the 5th lowest and highest values of the summary statistic from 199 Monte Carlo simulations of the null model. All analyses were performed using the software Programita for point pattern analysis [40].

Results

Univariate analysis of _U. pumila_ trees

As shown in Fig 3 (see S1 Fig), old _U. pumila_ trees were randomly distributed at all scales within all 3 plots, medium _U. pumila_ trees exhibited a significant aggregated trend within 0–2.5 m in all 3 plots, and seedlings were significantly aggregated within 0–3.5 m in plot 1, within a 0–18.5 m scale in plot 2 and within 0–6.5 m in plot 3. All 3 tree categories were randomly distributed at other scales within all 3 plots.

The univariate analysis of shrubs

As shown in Fig 4 (see S2 Fig), xerophytic shrubs were significantly aggregated within 0–5.5 m in plot 1, within 0–6.5 m in plot 2, and mesophytic shrubs showed a tendency for a significant
or insignificant aggregation within 0–23.5 m in plot 2 and within 0–29.5 m in plot 3. The two shrub categories were randomly distributed at other scales within all 3 plots.

**Bivariate spatial analysis of three *U. pumila* tree categories**

As shown in Fig 5 (see S3 Fig), old trees and medium trees showed a significant positive correlation within 0–4 m in plot 1 and plot 2 and weak positive correlation within 4–20 m and within 0–45 m in plot 2 and plot 3, respectively. Old trees and seedlings showed a significant positive correlation within 0–2 m in plot 1 and a significant negative correlation within 3–10 m and within 0–10 m in plot 2 and plot 3, respectively. However, they did not show a significant correlation at other scales. Medium trees and seedlings showed a significantly positive correlation within 0–3 m and within a 1–6 m scale in plot 1 and plot 2 and a significant negative correlation within 1–11 m in plot 3.
Bivariate spatial analysis of *U. pumila* tree categories and shrub categories

As shown in Fig 6 (see S4 Fig), old trees and xerophytic shrubs had a significant negative correlation within 5–10 m and a significant positive correlation within 3–11 m in plot 1 and plot 2, respectively; medium trees and xerophytic shrubs had a significant positive correlation within 0–10 m only in plot 1, and seedlings and xerophytic shrubs had a significant positive correlation within 0–2 m and 0–7 m in plot 1 and plot 2, respectively.

As shown in Fig 7 (see S4 Fig), old trees and mesophytic shrubs had a significant negative correlation within 0–20 m and within 1–15 m in plot 2 and plot 3, respectively. Medium trees and mesophytic shrubs had a significant negative correlation within 0–20 m and 0–40 m in plot 2 and plot 3, and seedlings and mesophytic shrubs had a significant negative correlation within 0–20 m and 0–19 m in plot 2 and plot 3, respectively.

**Discussion**

**Spatial patterns of woody plants and their mechanism of formation**

*U. pumila* trees. Tree species show different spatial patterns in their different growth stages and among the different age classes. These patterns are closely related to the self-thinning process, to the disturbance pattern (such as fire, grazing and so on) and to environmental change [42]. Analyzing the spatial patterns of different growth stages can yield information...
about the regeneration of new individuals, the morality of adults, and the overall demographics of a population following natural or human disturbance[43]. In general, young individuals aggregate, and adult individuals are randomly or uniformly distributed within a species [44]. In this study, old trees showed a random distribution, and medium *U. pumila* trees showed an aggregated distribution (0–2.5 m) in the smaller scales and a random distribution in the larger scales among all 3 plots. These patterns may result from the patchiness of water and soil resources at smaller scales in a semi-arid area[45]; however, these adult trees have formed a relatively stable structure in this type of temperate savanna despite differences in grazing intensity among the 3 plots, and their existence does not reduce the productivity of the herbaceous communities under their canopy [46]. These trees can, in turn, provide a shady resting habitat for domestic livestock during hot grazing seasons [47]. According to the results of Peng [36], two categories of old and medium adult trees have grown for more than 15 years; that is, the occurrence of these individuals, prior to the implementation of the alternative seasonal grazing-mowing regime, is a result of interactions among year-round free grazing and abiotic factors (such as climate, soil and microgeomorphology)[48]. There are fewer juvenile trees in all 3 plots, therefore their spatial pattern have not been analysed in this study (Table 1; Fig 8 and S5 Fig), the individual age of the juvenile tree category is less than 15 years old, which coincides
with the implementation period of the alternative seasonal grazing-mowing regime to a great extent; it can be deduced that the majority of one-year or multiyear seedlings that remained and grew from juveniles to adults\cite{49, 50} during the year-round free grazing procedure due to selective feeding of livestock, might be harvested by the nonselective mowing activity in autumn\cite{51–54}. This deduction can better explain why numerous seedlings (germinated

Fig 6. Bivariate spatial association between \textit{U. pumila} trees and xerophytic shrubs in plot 1 and plot 2 with the independent null model.

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Fig 7. Bivariate spatial association between *U. pumila* trees and mesophytic shrubs in plot 2 and plot 3 with the independent null model.

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mostly in the current year) existed in aggregations in our August investigation. This phenomenon interrupted the chain of normal regeneration of *U. pumila* trees. This severe human-caused disturbance, which may eventually result in the breakdown of the *U. pumila* tree community in the savanna ecosystem.

**Shrubs.** In arid and semi-arid systems, shrubs layers are often dominant [55–57], species rich, and are planted for revegetation in bare sand or less-covered soil surfaces in arid and semi-arid areas of China [58–60]. However, shrub encroachment into rangeland has been considered an obvious degradation indicator around the world for more than 20 years [61–65], despite some arguments appearing in recent years [66, 67]. In this study, shrubs occurred in the *U. pumila*-dominated savanna along the grazing gradient as xerophytic shrubs only in plot 1, as both xerophytic shrubs and mesophytic shrubs in plot 2, and as mesophytic shrubs only in plot 3. Additionally, the xerophytic shrubs showed significant aggregations at a smaller scale (0–8 m) in plot 1 and plot 2, while the mesophytic shrubs showed significant or insignificant aggregations at a larger scale (0–25 m) in plot 2 and plot 3. We are not sure when these shrubs encroached on the savanna, whether before or after the implementation of the new management regime (alternative seasonal grazing-mowing regime), but it can be deduced from related studies that their encroachment resulted from the grazing pressure on the one hand and from long-term climate change on the other hand [68–71]. Mowing operations can obviously cut shrub saplings and seedlings while also cutting *U. pumila* seedlings, as noted above, but the sprouting traits of some shrubs can facilitate their existence in a human-disturbed habitat [72–74]. Based on this phenomenon, we may deduce that *Betula fruticosa*, the only mesophytic and nonsprouting shrub in the study site, might have been established before the implementation of the new management regime, while most of the observed xerophytic shrubs with sprouting traits might have encroached on the savanna after the implementation of the new management regime.

**Spatial interactions among woody plants**

Among these three tree categories, there was a relatively weak positive correlation between old and medium trees in all 3 plots. Between the medium trees and seedlings, there was significant facilitation on a smaller scale in plot 1 and plot 2, which may result from wind-dispersed seed
deposition around medium trees and better micro-habitat provision for seed germination and seedling growth by medium trees\cite{75, 76}. In plot 3, significant competition at the 1–11 m scale occurred between medium trees and seedlings. This pattern may be the result of the occurrence of more seedlings around the medium trees due to the occurrence of less livestock trampling, associated with low grazing pressure \cite{77–79}.

Except in the case of the comparison between old trees and xerophytic shrubs in plot 1, facilitative relationships were significant between medium trees or seedlings and xerophytic shrubs in plot 1 and plot 2 (Fig 6). Significant competitive relationships were found among old trees, medium trees or seedling and mesophytic shrubs in plot 2 and plot 3 (Fig 7). These findings may result entirely from the exploitation of soil and water by plants with different ecophysiological traits \cite{80–82}. For the former, medium trees may act as nurse plants for xerophytic shrubs and seedlings, and xerophytic shrubs may also act as nurse plants for seedlings, in agreement with the “nurse plant syndrome” \cite{83–86}; for the latter, their similar ecophysiological traits require them to maintain competitive relationships under the influence of climate change \cite{87–89}.

In conclusion, the implementation of a new management regime resulted in xerophytic shrub encroachment or existence, which may result from a dual effect of seasonal grazing and climate change, and broke the chain of normal succession of a \textit{U. pumila} tree community in this typical temperate savanna ecosystem. Clearly, a new, commonly used (active or passive) management regime was used to replace the older traditional management regime. The new management regime might eventually result in the degradation of original tree-dominated savanna to xerophytic shrub-dominated savanna.

More field experiments should be undertaken to reveal underlying ecological processes (e.g. changes of soil and water) that gave rise to plant spatial pattern and to prove our deduction from pattern, and a more scientific and effective management regime should be studied to maintain the stability and sustainability of this typical tree-dominated savanna ecosystem in the present and near future.

**Supporting Information**

\textbf{S1 Fig.} This dataset contains a univariate analysis of the \textit{U. pumila} tree and of shrubs. (XLSX)

\textbf{S2 Fig.} This dataset contains a univariate analysis of shrubs. (XLSX)

\textbf{S3 Fig.} This dataset contains a bivariate spatial analysis including three \textit{U. pumila} tree categories. (XLSX)

\textbf{S4 Fig.} This dataset contains a bivariate spatial analysis including \textit{U. pumila} tree and shrubs. (XLSX)

\textbf{S5 Fig.} This dataset contains the proportion of different age-class categories of \textit{U. pumila} trees. (XLS)

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Author Contributions
Conceived and designed the experiments: KBZ JXZ. Performed the experiments: XW BZ. Analyzed the data: XW. Contributed reagents/materials/analysis tools: XW KBZ. Wrote the paper: XW KBZ JXZ BA.

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