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Article

Canopy structure: An intermediate factor regulating grassland diversity-function relationships under human disturbances

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A B S T R A C T

Grasslands are one of the largest coupled human-nature terrestrial ecosystems on Earth, and severe anthropogenic-induced grassland ecosystem function declines have been reported recently. Understanding factors influencing grassland ecosystem functions is critical for making sustainable management policies. Canopy structure is an important factor influencing plant growth through mediating within-canopy microclimate (e.g., light, water, and wind), and it is found coordinating tightly with plant species diversity to influence forest ecosystem functions. However, the role of canopy structure in regulating grassland ecosystem functions along with plant species diversity has been rarely investigated. Here, we investigated this problem by collecting field data from 170 field plots distributed along an over 2000 km transect across the northern agro-pastoral ecotone of China. Aboveground net primary productivity (ANPP) and resilience, two indicators of grassland ecosystem functions, were measured from field data and satellite remote sensing data. Terrestrial laser scanning data were collected to measure canopy structure (represented by mean height and canopy cover). Our results showed that plant species diversity was positively correlated to canopy structural traits, and negatively correlated to human activity intensity. Canopy structure was a significant indicator for ANPP and resilience, but their correlations were inconsistent under different human activity intensity levels. Compared to plant species diversity, canopy structural traits were better indicators for grassland ecosystem functions, especially for ANPP. Through structure equation modeling analyses, we found that plant species diversity did not have a direct influence on ANPP under human disturbances. Instead, it had a strong indirect effect on ANPP by altering canopy structural traits. As to resilience, plant species diversity had both a direct positive contribution and an indirect contribution through mediating canopy cover. This study highlights that canopy structure is an important intermediate factor regulating grassland diversity-function relationships under human disturbances, which should be included in future grassland monitoring and management.

1. Introduction

Grasslands are one of the most widely distributed and the largest coupled human-nature terrestrial ecosystems on Earth [1,2], comprising 80% of agriculturally productive lands and supporting around 40% of global agricultural domestic products [3]. Sustainably delivering grassland ecosystem functions and services is of great importance to humans and wildlife subsisting on them [2]. However, human activities (e.g., overgrazing, inappropriate agricultural practices, urbanization, mining) have led to severe grassland degradation, threatening their capabilities to reliably provide functions and services to humanity [4,5]. Understanding the change of grassland ecosystem functions in face of human activities is therefore critical for making sustainable management policies.

Aboveground net primary productivity (ANPP) and stability (the ability of ecosystems to maintain or restore their own structure and functions, which can be expressed as resistance, i.e., the magnitude of change after disturbances, or resilience, i.e., the ability returning to its original

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state after disturbances) are two key indicators of grassland ecosystem functionality [6,7]. Anthropogenic-induced plant species diversity loss is believed to be a major pathway influencing grassland ANPP and stability [8,9]. It is generally hypothesized that the increase of human activity intensity can reduce plant species diversity and therefore reduce grassland ANPP and stability [9–11]. Although the decrease of plant species diversity with the increase of human activity intensity has been widely reported by previous studies [12–14], the observed diversity-function relationships are inconsistent [2,15–19], leading to contradictory understandings on the effect of human activity intensity on grassland ecosystem functions [20]. Although ecological theories, e.g., the complementary effect and the insurance effect, have been successfully used to explain these inconsistent observations [2,16,19], we still lack a complete understanding on the exact processes leading to various anthropogenic-induced diversity-function relationships, limiting our capabilities to make appropriate management policies to enhance grassland ecosystem functionality.

Canopy structure, the three-dimensional morphological characteristic of vegetation canopy elements, is an important factor directly influencing grassland ecosystem functions [21–23]. Communities with more complex canopy structures intercept light more efficiently and conserve more water by reducing transpiration loss, and therefore generally result in higher ANPP [24,25]. For grasslands, where strong wind occurs frequently, the canopy with a higher surface roughness can also act as a physical barrier to resist wind-induced mechanical stress and therefore influences grassland stability [26,27]. With the change of plant species compositions and human activity intensity, canopy structure can be altered greatly [28,29]. Therefore, here we hypothesize that the influence of human activities on grassland ecosystem functions is a superposition effect of anthropogenic-induced plant species diversity changes and their corresponding canopy structure changes, and canopy structure may serve as an intermediate factor linking plant species diversity and grassland ecosystem functions under human activities. This hypothesis has been proven in forest ecosystems where increases in plant species diversity can increase canopy structure complexity and therefore lead to a higher productivity [30]. However, how grassland canopy structure varies with plant species diversity under human activities has been rarely investigated, and whether canopy structure serves as a "bridging" factor mediating grassland diversity-function relationships under different human activity intensities remains unclear.

This study aims to test the abovementioned hypothesis by addressing the following three specific questions. (1) What are the correlations between grassland plant species diversity and canopy structural traits under different human activity intensities? (2) Can canopy structural traits and plant species diversity be used as predictors for grassland ANPP and stability under different human activity intensities? (3) How do canopy structural traits vary with plant species diversity to mediate grassland ecosystem ANPP and stability under human activities? A total of 170 field plots of 77 study sites distributed across the northern agro-pastoral ecotone of China with large latitude and longitude gradients were surveyed to collect plant species diversity and ANPP measurements. Moreover, the state-of-the-art terrestrial laser scanning (TLS) technique was used to quantify their canopy structural traits, and over 20-year monthly Moderate Resolution Imaging Spectroradiometer (MODIS) images with a resolution of 250 m were collected to quantify stability.

2. Materials and methods

2.1. Field measurements

In this study, we randomly selected 77 study sites across the northern agro-pastoral ecotone of China (36°2′34″–49°41′11″N, 104°20′25″–123°49′43″E) (Fig. 1), covering various grassland vegetation types (e.g., meadow steppe, typical steppe, and desert steppe). This region is in the arid and semi-arid transition climate zone with an average mean annual temperature (MAT) of around 2.5 °C and an average mean annual precipitation (MAP) of around 370 mm. It is characterized as an area with intense agricultural and pastoral activities and is highly sensitive to global climate change [31]. Maintaining grassland ecosystem functions under the background of global climate change has been a research and management focus of the region [31,32].

Within the 77 study sites, a total of 170 plots (1 m × 1 m) were randomly selected to collect field measurements (Fig. 1 and Table S1). The 28 plots in the eastern section of the region (zone A in Fig. 1) were surveyed in 2017, the 74 plots in the western section (zone B in Fig. 1) were surveyed in 2018, and the 68 plots in the northern section (zone C in Fig. 1) were surveyed in 2020. These plots were visited during the peak growing season (July and August) of each survey year, and each plot was ensured to be representative of the vegetation condition of its surrounding areas before being set up. Within each plot, plant species compositions were visually identified by experienced ecologists, and the number of individuals was manually counted for each plant species. Correspondingly, species richness, defined as the number of species in a community or habitat, was calculated to represent the plant species diversity of each plot. The location of each plot was recorded by a CHCNAV Global Navigation Satellite System receiver, which can provide a centimeter-level positioning accuracy through the aid of Qianxun continuously operating reference stations [33].

2.2. TLS data and canopy structural traits extraction

Within each plot, we collected TLS data using either a RIEGL VZ-400 laser scanner (RIEGL Laser Measurement System GmbH, Horn, Austria; in sections A and B) or a FARO Focus S70 3D laser scanner (Faro Technologies, Inc., Lake Mary, FL, US; in section C) (Fig. 1). RIEGL VZ-400 has a maximum measurement range of 400 m and a ranging accuracy of around 0.5 cm, and FARO Focus S70 3D has a maximum measurement range of 70 m and a ranging accuracy of up to 0.5 cm. Both TLS scanners have been used to extract grassland canopy structural traits accurately [23,33]. To match TLS data with field plot measurements, four high-reflectance targets were manually set up at the four corners of each plot, which were then visually identified from the collected TLS data and used as references to clip the data. The clipped TLS data of each plot were then preprocessed following the same streamlined procedure, including steps of denoising, filtering, and normalization [35,36]. Denoising aims to remove noise points caused by wind, high-flying objects (e.g., powerlines, birds), etc., and a *k*-nearest neighboring denoising algorithm described in Rusu and Cousins [37] was used in this study. Filtering aims to identify ground points, and a local minimum filtering algorithm described in Xu et al. [23] was adopted. Normalization aims to remove the influence of terrain on TLS height measurements by subtracting the height of a point by the height of its corresponding ground point [33]. The abovementioned preprocessing steps were all performed in the LiDAR360 software (GreenValley International Inc.).

From the normalized TLS data, two canopy structural traits (i.e., mean height and canopy cover) were extracted for each plot, because they were reported to be two important indicators for grassland canopy structural complexity in the vertical and horizontal dimensions and to be highly sensitive with grassland ecosystem function changes [23,33]. To calculate mean height and canopy cover, each plot was first divided into regular cells with a size of 5 cm × 5 cm [22,23]. Then, mean height was calculated as the average height of canopy surface points (i.e., points with maximum normalized heights in each cell) [33], and canopy cover was calculated as the ratio of vegetated cells (i.e., cells with more than 1 nonground points) to the total number of cells.

2.3. Grassland ecosystem functions

Two key indicators of grassland ecosystem functionality, i.e., ANPP and stability, were derived in this study. ANPP was represented by the dry weight of plant organs in each plot [38], which was obtained by first harvesting all plants falling inside a plot and then drying them at 65 °C

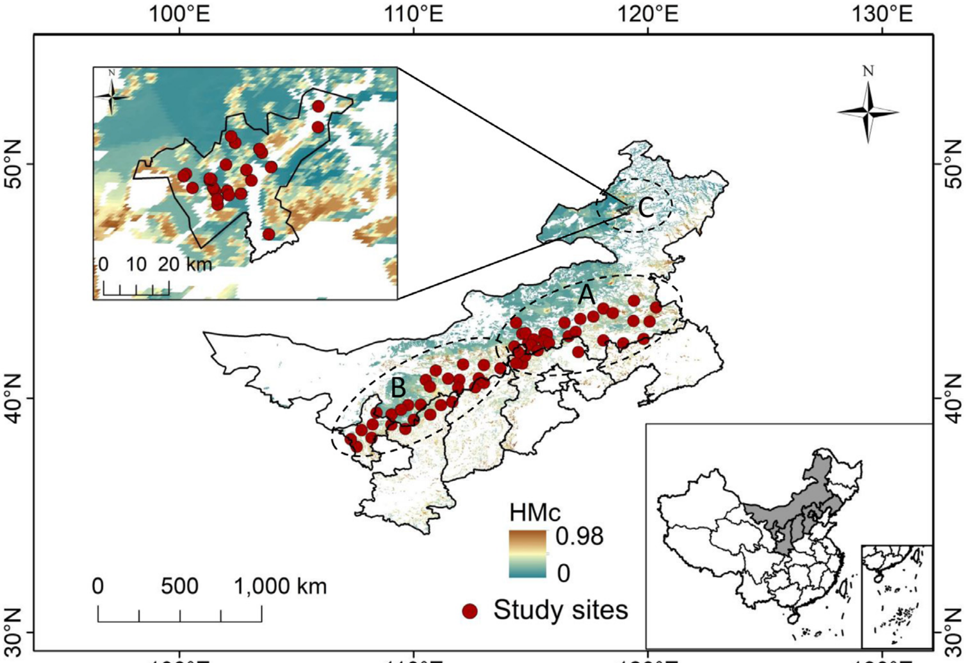

Fig. 1. An illustration of the study area location and the study site distribution. Zone A, B, and C represent eastern, western, and northern sections with study sites surveyed in 2017, 2018, and 2020, respectively. HMc in the background represents the 2015 cumulative human modification index with values ranging from 0 to 1 (1 represents the largest proportion of a landscape being modified by human activities, indicating a high human activity intensity) [34]. The maps were drawn based on the standard base map provided by the National Platform for Common Geospatial Information Service (GS (2020)1044).

until reaching a constant weight. Grassland stability was represented by resilience, the ability to return to the original state of an ecosystem after disturbances [6,7]. Because we did not have time-series field measurements, a method based on time-series satellite-derived normalized difference vegetation index (NDVI) was used, which assessed resilience through a composite of NDVI-derived early warning indicators [39]. In this study, the MOD13Q1.061 NDVI images from January 2000 to December 2020 (with a spatial resolution of 250 m and a temporal resolution of one day) were downloaded from the Google Earth Engine and used to calculate a resilience product covering the study area [41]. The calculation procedure of resilience can be found in Feng et al. [39] and is not described in detail here. Note that the NDVI values of each plot were temporally detrended before calculating resilence as suggested by Feng et al. [39] and Forzieri et al. [40]. The resilience of each plot was extracted from the calculated product based on its field-recorded location (Table S1). Although there was a scale mismatch between field measurements and satellite images (1 m × 1 m vs. 250 m × 250 m), the average coefficient of variation of NDVI values (derived from cloud-free Sentinel-2 images) within MODIS pixels was only 0.12, and 50% of the plots had a coefficient of variation smaller than 0.07 (Fig. S1a), indicating that vegetation conditions within plots were spatially homogeneous. In addition, there was a strong correlation ($R^2 = 0.91$) between MODIS-derived NDVI values and Sentinel-2 derived NDVI values (means within MODIS pixels) (Fig. S1b). Therefore, we believe that the MOD13Q1.061 NDVI images could be used to reflect the vegetation resilience of each plot.

2.4. Ancillary datasets

Two ancillary datasets were collected to evaluate the human activity intensity and climate conditions of each plot. Human activity intensity was represented by the 2015 cumulative human modification index (HMc) produced by Kennedy et al. [34]. HMc is presented as a continuous 0–1 metric considering 13 anthropogenic stressors that can directly or indirectly alter and impact natural lands, including human settlement (population density, and build-up area), agricultural (cropland, and livestock), transportation (major road, minor road, two-track, and railroad), mining and energy production (mining, oil well, wind turbine) and electrical infrastructure (powerline, and nighttime light) [34]. It was provided at a spatial resolution of 1 km, and a value closer to 1 represented a higher human activity intensity. In addition to directly using the original HMc value, we also categorized HMc into three groups, which were low intensity (HMc ≤ 0.10), moderate intensity (0.10 < HMc ≤ 0.40), and high intensity (HMc > 0.40) (Fig. 1), following the suggestion by Kennedy et al. [34]. There were 25, 95 and 50 plots in the groups of low, moderate and high intensities, respectively.

Climate conditions were derived from the WorldClim product, a widely used 1-km resolution climate surface for global land surfaces [42]. Here, we downloaded all available (the period from 1970 to 2000) monthly data for mean temperature and precipitation from the web (http://www.worldclim.org/), and calculated the average MAT and MAP from them to represent the climate conditions of the study area. The human activity intensity and climate conditions of each plot were extracted based on its field-recorded locations.

2.5. Statistical analyses

The simple linear regression method was used to investigate the relationships between plant species diversity and canopy structural traits. All 170 plots and plots from the low, moderate, and high human activity intensity groups (determined by HMc as described in Section 2.3) were fed to the simple linear regression models to evaluate how their correlations changed with human activity intensity, and the coefficient of determination (R^2) and the p-value (P) were reported for each model.

The simple linear regression method was also used to evaluate the correlations of grassland ecosystem functions with plant species diversity and canopy structural traits under different human activity intensity levels. Moreover, random forest was further used to determine nonlinear multivariate contributions of plant species diversity, canopy structural traits, and climate conditions to grassland ecosystem functions. Random

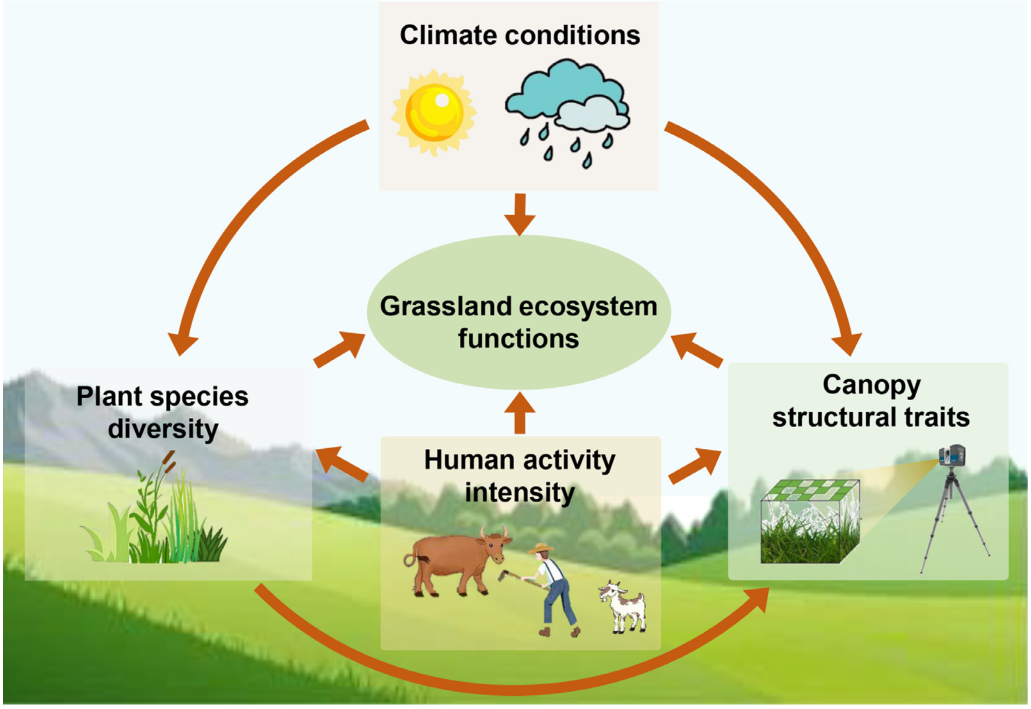

Fig. 2. The conceptual framework of structural equation models. The models evaluate the coordinated influence of plant species diversity, canopy structural traits, and climate conditions on grassland ecosystem functions under human disturbances.

forest is a non-parametric ensemble learning method for classification and regression tasks and can examine variable importance through a random permutation approach [43]. In this study, the number of trees and the number of variables tried at each split of each model were set as 500 and 2, and the relative variable importance was evaluated by the percentage increase of mean-squared error. Similar to simple linear regression analyses, eight random forest models (four for ANPP and four for resilience) were built by feeding all plots and plots from different human activity intensity groups using the R *RandomForest* package [43].

The structure equation modeling (SEM) method was used to examine how canopy structural traits mediate the grassland diversity-function relationships. SEM refers to a set of statistical modeling techniques aiming to measure and analyze casual relationships between observed and latent variables [44]. In this study, all obtained variables were used to build two separate SEM models (one for ANPP and one for resilience) using the R *lavaan* package [45], following the hypothesis that the influence of human activities on grassland ecosystem functions is a superposition effect of anthropogenic-induced plant species diversity changes and their corresponding canopy structure changes (Fig. 2). Standardized path coefficients and their P values were calculated to examine direct and indirect effects on grassland ecosystem functions. Insignificant paths ($P > 0.05$) were removed from the original SEM models to build two final models, and their adequacies were evaluated by P, the ratio of chi-square to degrees of freedom (χ^2/df), and the root mean square error of approximation (RMSEA). A large P (>0.05), a small χ^2/df (<3), and a small RMSEA (<0.08) indicate that there is no significant difference between the observed and modeled covariances, and the corresponding SEM model can be accepted [46].

3. Results

3.1. Relationships between grassland plant species diversity and canopy structural traits under human disturbances

Both mean height and canopy cover had significant positive correlations with species richness ($P < 0.001$), and the correlation of species richness with mean height was slightly stronger than that with canopy cover (Fig. 3). With species richness valued greater than 10, canopy cover stayed around 90% with small fluctuations, indicating there was a saturation effect in the relationship between them (Fig. 3b). Correlations of species richness with both mean height and canopy cover were the strongest in the moderate human activity intensity group ($R^2 = 0.25$ and 0.19, $P < 0.001$) (Fig. 3). With human activity intensity increasing from moderate to high, their correlations became weaker, and the drop of R^2 for canopy cover was much higher than that for mean height (Fig. 3). There were no significant correlations between species richness and mean height and canopy cover in the low human activity intensity group (Fig. 3).

3.2. Relationships of grassland ecosystem functions with plant species diversity and canopy structural traits under human disturbances

Both canopy structural traits and plant species diversity showed significant positive correlations with ANPP ($P < 0.001$), and mean height had the strongest correlation with ANPP ($R^2 = 0.53$), followed by canopy cover ($R^2 = 0.33$) and species richness ($R^2 = 0.24$) (Fig. 4a–c). The correlation between canopy cover and ANPP became strongly saturated after ANPP reached around 100 $g \cdot m^{-2} \cdot yr^{-1}$ (Fig. 4b). ANPP had the strongest correlations with mean height, canopy cover, and species richness in the moderate human activity intensity group, followed by the high human activity intensity group and low human activity intensity group (Fig. 4a–c). Mean height was the only factor having significant positive correlations with ANPP in all three human activity intensity groups (Fig. 4a).

Different from ANPP, resilience had no significant correlations with mean height and species richness overall, and it only had a weak positive correlation with canopy cover (Fig. 4d–f). However, in the moderate human activity intensity group, species richness and both canopy structural traits (i.e., mean height and canopy cover) had significant positive correlations with resilience, although their R^2 values were relatively small, ranging from 0.14 to 0.23 (Fig. 4d–f). Canopy cover was the only factor having a significant positive correlation with resilience in the low hu-

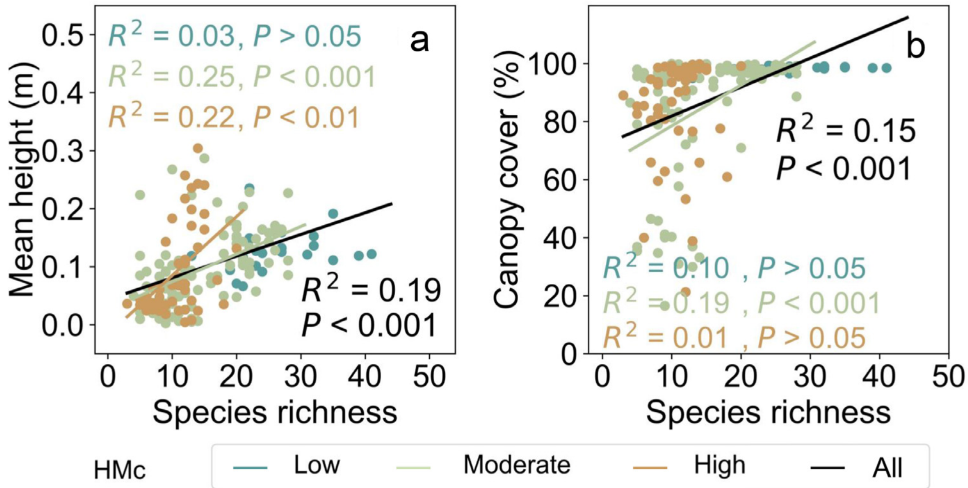

Fig. 3. Scatter plots (a) between species richness and mean height and (b) between species richness and canopy cover. Low, moderate, and high human activity intensity groups contain plots with a HMc ≤ 0.10, 0.10–0.40, and >0.40, respectively, and all represent results using all plots. R^2 represents the coefficient of determination, and P represents the p-value of statistical tests. The solid line of each human activity intensity group is the fitted line. Note that only fitted lines with a $P \leq 0.05$ are presented here.

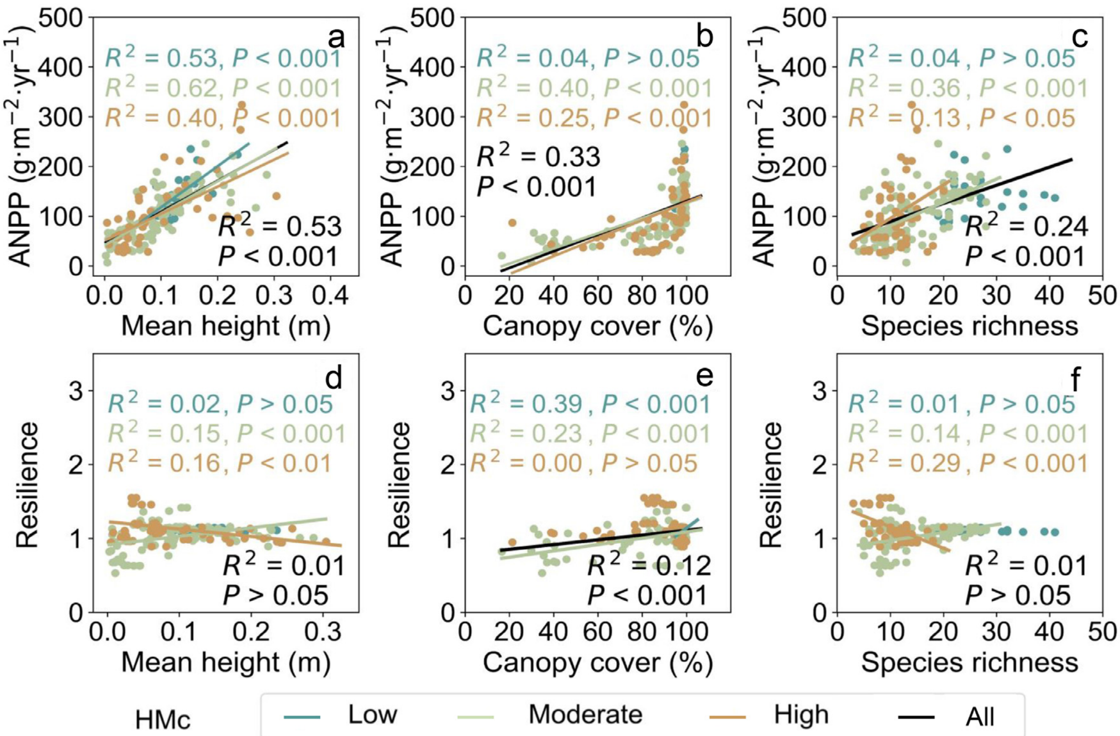

Fig. 4. Scatter plots (a-c) between ANPP and mean height, canopy cover, and species richness, and (d-f) between resilience and mean height, canopy cover, and species richness. ANPP represents aboveground net primary productivity. The solid line of each human activity intensity group is the fitted line. Note that only fitted lines with a $P \leq 0.05$ are presented here.

man activity intensity group (Fig. 4e), and both mean height and species richness had significant negative correlations with resilience in the high human activity intensity group (Fig. 4d,f). With the increase of human activity intensity, the correlation between resilience and species richness and mean height became stronger, while the correlation between resilience and canopy cover became weaker (Fig. 4d–f).

Based on random forest analyses, canopy structural traits were the most influential factors on ANPP, followed by MAP, species richness, and MAT (Fig. 5a). With human activity intensity increasing from low to high, mean height kept being one of the most important factors influencing ANPP, and the variable importance of canopy cover increased significantly (Fig. 5a); while the variable importance of species richness decreased with human activity intensity (Fig. 5a). The influence of climate conditions on ANPP stayed relatively stable with the variation of human activity intensity (Fig. 5a). As to resilience, canopy structural traits (i.e., mean height and canopy cover) and climate conditions (i.e., MAT and MAP) were the more influential factors (Fig. 5b). MAP kept being one of the most important factors influencing resilience in all human activity intensity groups (Fig. 5b). The variable importance of canopy cover increased significantly with human activity intensity,

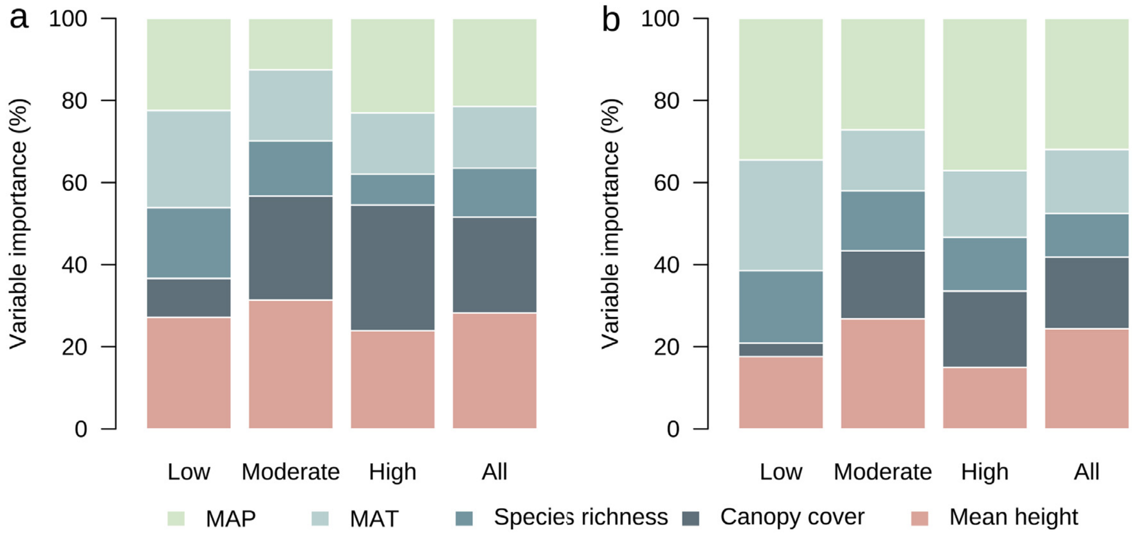

Fig. 5. Random forest-derived variable importance for predicting (a) ANPP and (b) resilience using plots under different human activity intensity levels (i.e., low, moderate, high). MAT and MAP represent mean annual temperature and mean annual precipitation, and All represents random forest analyses using all plot measurements.

and that of species richness decreased (Fig. 5b). The variable importance of mean height was the highest in the moderate human activity intensity group.

3.3. Coordinated influence of plant species diversity and canopy structural traits on grassland ecosystem functions under human disturbances

The coordinated influence of species richness and canopy structural traits on grassland ANPP and resilience under human disturbances were evaluated using the SEM method. The SEM models for both ANPP and resilience had a *P* value larger than 0.05, a χ^2/df smaller than 3, and a RMSEA smaller than 0.08, indicating that they were statistically sound (Fig. 6). Both climate conditions and human activity intensity had a direct influence on species richness, and the contribution of MAT was the strongest (Fig. 6). Species richness decreased with human activity intensity and MAT, while increased with MAP (Fig. 6). Both species richness and human activity intensity had direct positive contributions to mean height and canopy cover, but the contributions of species richness were much stronger than human activity intensity (Fig. 6). In addition to the direct contribution, human activity intensity also indirectly contributed to mean height and canopy cover by altering species richness, and interestingly the indirect contribution (negative) was opposite to the direct contribution (positive) (Fig. 6). Climate conditions mainly indirectly contributed to mean height and canopy cover through altering species richness, and only MAP had a weak direct positive contribution to mean height (Fig. 6).

The coordination of species richness and canopy structural traits as well as the direct influence of climate conditions explained 62% of variations of grassland ANPP under human disturbances (Fig. 6a). Mean height had the greatest direct contribution to ANPP (positive), followed by MAP (positive), canopy cover (positive), and MAT (negative) (Fig. 6a and Table S2). Species richness did not have a direct influence on ANPP. Instead, it contributed to ANPP by mediating canopy structural traits, especially by altering canopy height (Fig. 6a). The coordination of species richness and canopy structural traits as well as the direct influences of climate conditions and human activities explained 42% variations of grassland resilience (Fig. 6b). MAP had the strongest direct contribution to resilience (negative), followed by human activity intensity (positive), canopy cover (positive), species richness (positive), and MAT (negative) (Fig. 6b and Table S3). Species richness had a direct influence on resilience and it also contributed to resilience by mediating canopy cover (Fig. 6b). Mean height did not have a direct influence on resilience (Fig. 6b).

4. Discussion

In this study, we evaluated the influence of plant species diversity and canopy structural traits on grassland ecosystem functions (i.e., ANPP and Resilience) under human disturbances using field measurements and TLS data distributed across the northern agro-pastoral ecotone of China with large latitude and longitude gradients. The study area is in the arid and semi-arid transition climate zone, which is highly sensitive to climate change [4,32,47]. The plant species diversity of the region is mainly controlled by climate conditions, especially MAT (Figs. 6 and S2). MAP contributes to species richness positively (Figs. 6 and S2), which is possibly caused by the fact that this region is water-limited, and the increase of water availability may improve the site condition for plant growth [48–50]. MAT contributes to species richness negatively, and its contribution is stronger than MAP (Figs. 6 and S2). This might be caused by the fact that the variation of MAP in the study area is relatively small (Fig. S3), and the decrease of MAT possibly reduces the magnitude of water loss through the evapotranspiration process [51–53]. Human activity can lead to plant species diversity loss (Fig. 6), similar to findings from previous studies [9].

Mean height and canopy cover are two important grassland canopy structural traits that can represent the canopy horizontal and vertical structural information, which have been used as indicators for plant species diversity [29]. In this study, we did observe significant positive correlations between species richness and mean height and canopy cover (Figs. 3 and 6), but their correlations varied with human activity intensity (Fig. 3). The strongest correlations were observed in the moderate human activity intensity group (Fig. 3). The relatively low correlations in the high human activity group are possibly caused by the phenomenon of a few plant species dominating an area to form a tall and closed canopy (Figs. 3 and S4). Fundamentally, in areas with high human activity intensity, site conditions (e.g., soil) might have been altered greatly due to severe grassland degradation [54], and certain plant species (e.g., *Artemisia* L., a widely distributed plant species in severely degraded grassland) might be better adapted to these changes [51], leading to a higher frequency of occurrence for this phenomenon. The positive direct contributions of human activity intensity to mean height and canopy cover in SEM models might be caused by this phe-

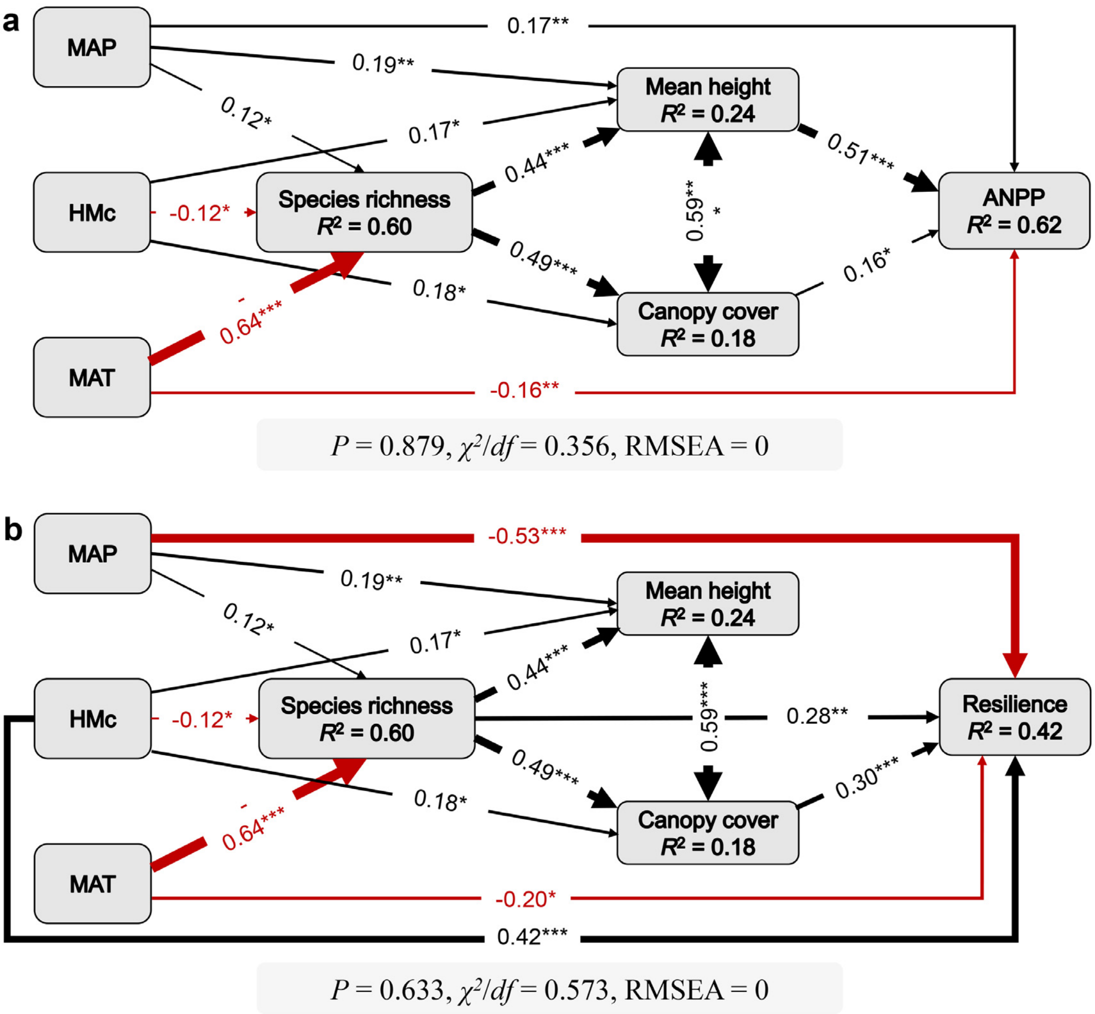

Fig. 6. The coordination effect of species richness, canopy structural traits, and climate conditions on (a) ANPP and (b) resilience under human disturbances. Black and red solid lines denote significant positive and negative paths ($P < 0.05$), and the numbers on them represent standardized path coefficients. χ^2/df represents the ratio of chi-square to degrees of freedom, and RMSEA represents the root mean square error of approximation. Information on unstandardized path coefficients is provided in Tables S2 and S3.

nomenon as well (Fig. 6). The insignificant correlations in the low human activity intensity group might be caused by the fact that plots of this group are mainly clustered in the northern section (zone C in Fig. 1), which have similar plant species compositions with relatively small variations in species richness (Table S1). Moreover, in the study area, climate conditions have relatively weak or insignificant direct contributions to mean height and canopy cover and mainly indirectly influence them through altering species richness (Fig. 6), which further manifests the importance of plant species diversity in regulating canopy structure in degraded grasslands.

Canopy structural traits have the strongest direct contributions to grassland ANPP (Fig. 6a), and mean height is the only factor having a significant positive correlation with ANPP under all human activity intensity levels (Fig. 4a), indicating they could be used as reliable indicators to predict ANPP [23,55]. Although species richness has a significant positive correlation with ANPP, their correlation varies with human activity intensity and its contribution is indirect (Figs. 4a and 6a). This might explain the inconsistent observations between plant species diversity and ANPP in previous studies [15,17–19]. Human activities can lead to losses in plant species diversity, and therefore reduce grassland ANPP by reducing mean height and canopy cover (Fig. 6a). However, when the reduction of mean height and canopy cover exceeds a certain tipping point, it may lead to severe grassland degradation (e.g., desertification) in the arid and semiarid regions [56]. Then as mentioned above, the appearance of certain plant species adapted to these changes can still generate high ANPP by forming tall and closed grassland canopy (Fig. S4), leading to inconsistent correlations between plant species diversity and ANPP. The increasing variable importance of canopy structural traits with human activity intensity in the random forest analyses further suggests the importance of canopy structure in regulating the anthropogenic-induced grassland diversity-ANPP relationship (Fig. 5a). Besides the coordinated effect of anthropogenic-induced plant species diversity and canopy structure changes on grassland ANPP, climate conditions also have direct contributions to ANPP, but their contributions are modest (Fig. 6a).

Ecosystem stability can be expressed as the resistance to disturbances (i.e., the magnitude of change after disturbances) or the resilience after disturbances (i.e., the ability returning to its original state) [6,7]. Considering the fact that the calculation of resistance requires a specific disturbance event that can be hardly specified in this study and the study area is dominated by annual plants that are easily influenced by climate conditions [52], resilience might be a more appropriate indicator for grassland ecosystem stability in this study. The contributions of species richness and canopy structural traits to resilience vary significantly among human activity intensity groups with a similar pattern, and their overall contributions are weak or insignificant (Fig. 4d–f). The positive contribution of species richness and canopy structural traits to resilience in the low/moderate human activity intensity group might be explained by the insurance effect. Increases in plant species diversity can raise the spatial asynchrony (in terms of both species and canopy structure) through the insurance effect, which therefore improves resilience [2]. The insurance effect may be also the reason for species richness having both direct and indirect (through mediating canopy cover) contributions to resilience in the SEM analysis (Fig. 6b). However, in an extremely degraded grassland with high human activity intensity, it significantly altered site condition may not have enough resources to support the growth of a complex grassland ecosystem, and therefore reducing ecosystem complexity (in both species and structure) may be beneficial for maintaining its ecosystem stability [57]. The insignificant contribution of mean height to resilience in the SEM analysis might be caused by the superposition effect of the two abovementioned phenomena (Fig. 6b). Moreover, climate conditions have much stronger direct contributions to resilience than to ANPP. The negative direct contributions of MAT and MAP to resilence indicate that areas with better site conditions (higher MAP and MAT) might be more easily influenced by disturbance events (Fig. 6b), and the positive direct contribution of human activity intensity to resilience might be related to intermediate disturbance hypothesis [58].

Grassland diversity-function relationship in face of human activities is a key to making sustainable management policies, but inconsistent relationships have been reported in different studies [2,15–19]. This study highlights that canopy structure plays a critical role in mediating the diversity-function relationship in areas with different human activity intensities. Nevertheless, the mediating role of canopy structure (i.e., differences in regression slopes of their correlations with species richness and functional traits) might be contaminated by climate conditions. To address this issue, the Chow test, a statistical test that can examine whether two regression slopes between multiple sets of data have significant differences [59], is used to evaluate whether the influence of human activity intensity on regression slopes was significant. Detailed information on the Chow test is provided in Box S1. Without considering climate conditions, regression slopes of correlation between canopy structural traits and species richness and functional traits have significant differences in at least one pair of human activity intensity groups, except those between canopy cover and species richness (Table S4). After considering climate conditions, six out of the eight correlations between canopy structural traits and species richness and functional traits still have significant differences in regression slopes (Table S5). These suggest that human activity intensity is a significant factor influencing the correlations between canopy structural traits and species richness and functional traits, it is not contaminated by climate conditions.

Considering the critical role of canopy structure in mediating grassland diversity-function relationship, here we argue that the inclusion of canopy structure measurements in grassland monitoring is highly necessary not only for understanding grassland ecosystem processes in face of human activities, but also for grassland ecosystem monitoring and management. Although the recent development of light detection and ranging technology (lidar) enables accurate nondestructive measurements of canopy structural traits [55,60,61], there are still several limitations that need to be addressed in future studies. Firstly, the accuracy of lidar-based canopy structural traits measurements still needs to be improved, especially for certain traits that have been reported to be important factors influencing ecosystem processes, e.g., canopy structural complexity [25,57]. Secondly, large spatial/temporal scale mismatches are commonly seen between lidar measurements and field and satellite measurements, which is also the case in this study. Recently, there are high-resolution satellite images with high temporal frequency commercially available, e.g., PlanetScope, which may provide a solution to address the scale-mismatch issue. However, their capabilities in quantifying grassland resilience still need further investigations, especially considering their inconsistencies in digital number scaling [62,63]. Moreover, conducting repeated field surveys (including lidar) and developing methods to measure large-scale time-series grassland plant species diversity and canopy structure through the fusion of multisource remote sensing datasets (e.g., spaceborne lidar, hyperspectral data, radar data) are also urgently needed.

5. Conclusion

This study investigated the coordinated influence of plant species diversity and canopy structural traits on grassland ecosystem functions by surveying and analyzing data from 170 field plots distributed across the northern agro-pastoral ecotone of China. Overall, the plant species diversity of the study area is mainly controlled by climate conditions. Canopy structural traits have significant positive correlations with plant species diversity, but their correlations may vary with human activity intensity. Canopy structural traits, especially mean height, are stronger indicators for grassland ANPP than plant species diversity in all human activity intensity groups, but their correlations with grassland resilience are relatively weak and may vary with human activity intensity. Plant species diversity contributes to grassland ANPP indirectly through mediating canopy structural traits under human disturbances, and contributes to grassland resilience both directly and indirectly through mediating canopy cover. This study manifests that canopy structure is an important factor correlated to grassland plant species diversity and ecosystem functions and works as an intermediate factor regulating grassland diversity-function relationships under human disturbances. We argue that canopy structural traits should be considered in the formulation process of grassland management policies.

Declaration of competing interest

The authors declare that they have no conflicts of interest in this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.fmre.2022.10.007.

References

[1] M.J. Hovenden, P.C.D. Newton, Variability in precipitation seasonality limits grassland biomass responses to rising CO_2: historical and projected climate analyses, Clim. Chang. 149 (2) (2018) 219–231.
[2] M. Liang, C. Liang, Y. Hautier, et al., Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales, Ecol. Lett. 24 (10) (2021) 2054–2064.
[3] M. Herrero, P.K. Thornton, Livestock and global change: emerging issues for sustainable food systems, Proc. Natl. Acad. Sci. U. S. A. 110 (52) (2013) 20878–20881.
[4] T. Fetzel, P. Havlik, M. Herrero, et al., Seasonality constraints to livestock grazing intensity, Glob. Chang. Biol. 23 (4) (2017) 1636–1647.
[5] M.W. Liang, E.S. Gornish, Rainfall regulation of grazed grasslands, Proc. Natl. Acad. Sci. U. S. A. 116 (48) (2019) 23887–23888.
[6] A.A. Batabyal, H. Beladi, The stability of stochastic systems: the case of persistence and resilience, Math. Comput. Model. 30 (7–8) (1999) 27–34.
[7] V. Dakos, S. Kefi, Ecological resilience: what to measure and how, Environ. Res. Lett. 17 (4) (2022) 043003.
[8] M.D. Smith, A.K. Knapp, Dominant species maintain ecosystem function with non-random species loss, Ecol. Lett. 6 (6) (2003) 509–517.
[9] Y. Hautier, D. Tilman, F. Isbell, et al., Anthropogenic environmental changes affect ecosystem stability via biodiversity, Science 348 (6232) (2015) 336–340.
[10] Y. Bai, J. Wu, Q. Pan, et al., Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe, J. Appl. Ecol. 44 (5) (2007) 1023–1034.
[11] J. Qin, H. Ren, G. Han, et al., Grazing reduces the temporal stability of temperate grasslands in northern China, Flora 259 (2019) 151450.
[12] Y. Osem, A. Perevolotsky, J. Kigel, Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity, J. Ecol. 90 (6) (2002) 936–946.

[13] A. Narantsetseg, S. Kang, B.-E. Lkhamsuren, et al., Assessment of biotic and abiotic factors controlling herbaceous biodiversity in Mongolian steppes, Ecol. Inform. 29 (2015) 221–229.
[14] V.H. Klaus, D. Schafer, T. Kleinebecker, et al., Enriching plant diversity in grasslands by large-scale experimental sward disturbance and seed addition along gradients of land-use intensity, J. Plant Ecol. 10 (4) (2017) 581–591.
[15] P.B. Adler, E.W. Seabloom, E.T. Borer, et al., Productivity is a poor predictor of plant species richness, Science 333 (6050) (2011) 1750–1753.
[16] D.R. Chalcraft, Changes in ecological stability across realistic biodiversity gradients depend on spatial scale, Glob. Ecol. Biogeogr. 22 (1) (2013) 19–28.
[17] L.H. Fraser, J. Pither, A. Jentsch, et al., Worldwide evidence of a unimodal relationship between productivity and plant species richness, Science 349 (6245) (2015) 302–305.
[18] J.B. Grace, T.M. Anderson, E.W. Seabloom, et al., Integrative modelling reveals mechanisms linking productivity and plant species richness, Nature 529 (7586) (2016) 390–393.
[19] Q. Pan, A.J. Symstad, Y. Bai, et al., Biodiversity-productivity relationships in a natural grassland community vary under diversity loss scenarios, J. Ecol. 110 (1) (2021) 210–220.
[20] A. Hector, Y. Hautier, P. Saner, et al., General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding, Ecology 91 (8) (2010) 2213–2220.
[21] J. Wijesingha, T. Moeckel, F. Hensgen, et al., Evaluation of 3D point cloud-based models for the prediction of grassland biomass, Int. J. Appl. Earth Obs. Geoinf. 78 (2019) 352–359.
[22] D. Schulze-Brueninghoff, M. Wachendorf, T. Astor, Remote sensing data fusion as a tool for biomass prediction in extensive grasslands invaded by L. polyphyllus, Remote Sens. Ecol. Conserv. 7 (2) (2020) 198–213.
[23] K. Xu, Y. Su, J. Liu, et al., Estimation of degraded grassland aboveground biomass using machine learning methods from terrestrial laser scanning data, Ecol. Indic. 108 (2020) 105747.
[24] J. Sapijanskas, A. Paquette, C. Potvin, et al., Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences, Ecology 95 (9) (2014) 2479–2492.
[25] K. Rissanen, M.-O. Martin-Guay, A.-S. Riopel-Bouvier, et al., Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy, Agric. For. Meteorol. 278 (2019) 107655.
[26] Z. Guo, N. Huang, Z. Dong, et al., Wind erosion induced soil degradation in Northern China: status, measures and perspective, Sustainability 6 (12) (2014) 8951–8966.
[27] P. Li, E.J. Sayer, Z. Jia, et al., Deepened snow cover mitigates soil carbon loss from intensive land-use in a semi-arid temperate grassland, Funct. Ecol. 36 (3) (2022) 635–645.
[28] E.A. LaRue, B.S. Hardiman, J.M. Elliott, et al., Structural diversity as a predictor of ecosystem function, Environ. Res. Lett. 14 (11) (2019) 114011.
[29] C. Guimaraes-Steinicke, A. Weigelt, R. Proulx, et al., Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities, J. Ecol. 109 (5) (2021) 1969–1985.
[30] C.M. Gough, J.W. Atkins, R.T. Fahey, et al., High rates of primary production in structurally complex forests, Ecology 100 (10) (2019) e02864.
[31] Y. Yang, K. Wang, The effects of different land use patterns on the microclimate and ecosystem services in the agro-pastoral ecotone of Northern China, Ecol. Indic. 106 (2019) 105522.
[32] W. Chen, A. Li, Y. Hu, et al., Exploring the long-term vegetation dynamics of different ecological zones in the farming-pastoral ecotone in northern China, Environ. Sci. Pollut. Res. 28 (22) (2021) 27914–27932.
[33] X. Zhao, Y. Su, T. Hu, et al., Analysis of UAV lidar information loss and its influence on the estimation accuracy of structural and functional traits in a meadow steppe, Ecol. Indic. 135 (2022) 108515.
[34] C.M. Kennedy, J.R. Oakleaf, D.M. Theobald, et al., Managing the middle: a shift in conservation priorities based on the global human modification gradient, Glob. Chang. Biol. 25 (3) (2019) 811–826.
[35] X. Zhao, Q. Guo, Y. Su, et al., Improved progressive TIN densification filtering algorithm for airborne LiDAR data in forested areas, ISPRS J. Photogramm. Remote Sens. 117 (2016) 79–91.
[36] Y. Su, F. Wu, Z. Ao, et al., Evaluating maize phenotype dynamics under drought stress using terrestrial lidar, Plant Methods 15 (1) (2019) 1–16.
[37] R.B. Rusu, S. Cousins, Ieee, 3D is here: point cloud library (PCL), in: Proceedings of the IEEE International Conference on Robotics and Automation (ICRA), Shanghai, Peoples R China, 2011.
[38] H. Li, Z. Xu, Q. Yan, et al., Soil microbial beta-diversity is linked with compositional variation in aboveground plant biomass in a semi-arid grassland, Plant Soil 423 (1–2) (2018) 465–480.
[39] Y. Feng, H. Su, Z. Tang, et al., Reduced resilience of terrestrial ecosystems locally is not reflected on a global scale, Commun. Earth Environ. 2 (1) (2021) 88.
[40] G. Forzieri, V. Dakos, N.G. McDowell, et al., Emerging signals of declining forest resilience under climate change, Nature 608 (7923) (2022) 534–539.
[41] K. Didan, MODIS/Terra Vegetation Indices 16-Day L3 Global 250 m SIN Grid V061 [dataset]. NASA EOSDIS Land Processes DAAC. [en línea] [fecha de consulta: 18 de Junio de 2021 en] (2021), doi:10.5067/MODIS/MOD13Q1.061.
[42] S.E. Fick, R.J. Hijmans, WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas, Int. J. Climatol. 37 (12) (2017) 4302–4315.
[43] L. Breiman, Random forests, Mach. Learn. 45 (1) (2001) 5–32.
[44] K.A. Markus, Principles and practice of structural equation modeling, Struct. Equ. Model. Multidiscip. J. 19 (3) (2012) 509–512.
[45] Y. Rosseel, lavaan: an R package for structural equation modeling, J. Stat. Softw. 48 (2) (2012) 1–36.
[46] Y. Su, T. Hu, Y. Wang, et al., Large-scale geographical variations and climatic controls on crown architecture traits, J. Geophys. Res. Biogeosci. 125 (2) (2020) e2019JG005306.
[47] L.L. Sloat, J.S. Gerber, L.H. Samberg, et al., Increasing importance of precipitation variability on global livestock grazing lands, Nat. Clim. Chang. 8 (3) (2018) 214–218.
[48] K.B. Suttle, M.A. Thomsen, M.E. Power, Species interactions reverse grassland responses to changing climate, Science 315 (5812) (2007) 640–642.
[49] H. Yang, M. Wu, W. Liu, et al., Community structure and composition in response to climate change in a temperate steppe, Glob. Chang. Biol. 17 (1) (2011) 452–465.
[50] D. Liu, C. Zhang, R. Ogaya, et al., Increasing climatic sensitivity of global grassland vegetation biomass and species diversity correlates with water availability, New Phytol. 230 (5) (2021) 1761–1771.
[51] D. Han, G. Wang, B. Xue, et al., Evaluation of semiarid grassland degradation in North China from multiple perspectives, Ecol. Eng. 112 (2018) 41–50.
[52] L. Bai, Z. Wang, Y. Lu, et al., Monthly rather than annual climate variation determines plant diversity change in four temperate grassland nature reserves, Environ. Sci. Pollut. Res. 29 (7) (2022) 10357–10365.
[53] J. Shao, X. Zhou, K.J. Groenigen, et al., Warming effects on grassland productivity depend on plant diversity, Glob. Ecol. Biogeogr. 31 (3) (2022) 588–598.
[54] Q.-M. Dong, X.-Q. Zhao, G.-L. Wu, et al., A review of formation mechanism and restoration measures of "black-soil-type" degraded grassland in the Qinghai-Tibetan Plateau, Environ. Earth Sci. 70 (5) (2013) 2359–2370.
[55] D. Schulze-Brüninghoff, F. Hensgen, M. Wachendorf, et al., Methods for LiDAR-based estimation of extensive grassland biomass, Comput. Electron. Agric. 156 (2019) 693–699.
[56] C. Li, R. de Jong, B. Schmid, et al., Changes in grassland cover and in its spatial heterogeneity indicate degradation on the Qinghai-Tibetan Plateau, Ecol. Indic. 119 (2020) 106641.
[57] Y. Yonatan, G. Amit, J. Friedman, et al., Complexity-stability trade-off in empirical microbial ecosystems, Nat. Ecol. Evol. 6 (6) (2022) 693–700.
[58] J.F. Molino, D. Sabatier, Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis, Science 294 (5547) (2001) 1702–1704.
[59] S. Cleary, The relationship between firm investment and financial status, J. Financ. 54 (2) (1999) 673–692.
[60] Q. Guo, Y. Su, T. Hu, et al., Lidar boosts 3D ecological observations and modelings: a review and perspective, IEEE Geosci. Remote Sens. Mag. 9 (1) (2021) 232–257.
[61] T. Hu, X. Sun, Y. Su, et al., Development and performance evaluation of a very low-cost UAV-lidar system for forestry applications, Remote Sens. 13 (1) (2021) 77 (Basel).
[62] R. Houborg, M.F. McCabe, A cubesat enabled spatio-temporal enhancement method (CESTEM) utilizing planet, landsat and MODIS data, Remote Sens. Environ. 209 (2018) 211–226.
[63] J. Wang, D.D. Yang, M. Detto, et al., Multi-scale integration of satellite remote sensing improves characterization of dry-season green-up in an Amazon tropical evergreen forest, Remote Sens. Environ. 246 (2020) 111865.

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