Relationship Between Species and Life-Form Richness and Aboveground and Belowground Biomass in Alpine Meadows under Grazing Disturbance (Postprint)

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Abstract

To clarify the correlation between plant richness and biomass in alpine meadows under grazing disturbance and to provide a basis for predicting biomass of grassland plants at different growth stages, six grazing intensity plots were established with grazing continued for three consecutive years. In 2014, plant richness and above- and below-ground biomass were surveyed across three seasons (June, August, October), and the correlations between species and life-form richness (types of life forms) with above- and below-ground biomass under grazing disturbance were comparatively analyzed. The results showed: (1) Both species and life-form richness, as well as above-ground biomass, were significantly affected by grazing intensity. Species richness was significantly negatively correlated with grazing intensity only in August, life-form richness exhibited unimodal variation with grazing intensity in October, above-ground biomass was significantly negatively correlated with grazing intensity across all seasons, whereas below-ground biomass was unrelated to grazing intensity. (2) Species richness and both above- and below-ground biomass were significantly affected by season. Species richness and above-ground biomass showed unimodal variation with season only in low-intensity grazing areas, while below-ground biomass showed unimodal variation with season in moderate-intensity grazing areas; life-form richness was unrelated to season. (3) Before grazing disturbance, both species and life-form richness were significantly positively correlated with above- and below-ground biomass. After three years of grazing, only in August was species richness significantly positively correlated with above-ground biomass alone, whereas life-form richness was significantly positively correlated with both above- and below-ground biomass. (4) Across different grazing intensities, species richness was significantly positively correlated with above-ground biomass only in low-intensity grazing areas, whereas life-form richness was significantly positively correlated with above-ground biomass across all grazing intensity areas. In summary, grazing disturbance disrupted the relationship between richness and biomass in alpine meadows, particularly affecting the correlation between species richness and below-ground biomass. The significant relationship between life-form richness and above-ground biomass was not interfered with by grazing intensity, demonstrating the advantage of life-form richness in biomass prediction.

Full Text

Preamble

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Relationships Between Plant Species Richness, Lifeform Richness, and Above- and Below-ground Biomass Under Grazing Disturbance in an Alpine Meadow

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Abstract: Understanding the relationships between plant richness and biomass under grazing disturbance is crucial for predicting biomass during different plant growth periods. This study conducted a controlled grazing experiment with six grazing intensities in an alpine meadow in the eastern Qilian Mountains from 2012 to 2014. We investigated species richness, lifeform richness, and above- and below-ground biomass across three grazing seasons (June, August, and October), and analyzed the relationships between these variables under different grazing intensities. The results showed: (1) Species richness, lifeform richness, and aboveground biomass were significantly affected by grazing intensity. Species richness was negatively correlated with grazing intensity only in August, whereas lifeform richness showed a single-peak trend with grazing intensity in October. Aboveground biomass was significantly negatively correlated with grazing intensity across seasons, while belowground biomass showed no relationship with grazing intensity. (2) Species richness and above- and below-ground biomass were significantly affected by season. Species richness and aboveground biomass showed a single-peak change with season only in low-intensity grazing plots, while belowground biomass showed a single-peak change with season only in medium-intensity grazing plots. Lifeform richness showed no relationship with season. (3) Before grazing disturbance, both species and lifeform richness were significantly positively correlated with above- and below-ground biomass. After three years of grazing, species richness was positively correlated only with aboveground biomass in August, while lifeform richness was positively correlated with both above- and below-ground biomass in August. (4) Among different grazing intensity plots, species richness was significantly positively correlated with aboveground biomass only in low-intensity plots, whereas lifeform richness was positively correlated with aboveground biomass across all grazing intensity plots. In conclusion, grazing disturbance disrupted the relationship between plant richness and biomass in alpine meadows, particularly affecting the correlation between species richness and belowground biomass. However, the significant relationship between lifeform richness and aboveground biomass was unaffected by grazing intensity, demonstrating that lifeform richness shows superiority in determining biomass in alpine meadows.

Keywords: alpine meadow; grazing disturbance; species richness; lifeform richness; biomass

Introduction

The relationship between biodiversity and ecosystem functioning represents a central focus in contemporary ecological research. Biomass serves as a direct indicator of grassland ecosystem productivity and provides an effective pathway for studying biodiversity-ecosystem function relationships. Species diversity, as the manifestation of biodiversity at the species level, plays a decisive role in ecosystem productive functions and has been widely applied in biodiversity-productivity research. Plant functional groups, defined as assemblages of species with specific functional traits, represent an ecological concept introduced by researchers to study vegetation responses to environmental change and disturbance. Functional group diversity, which quantifies the number of species assemblages, simplifies the complexity of community species research and has been utilized in numerous studies.

However, for grassland ecosystems, which factor—species diversity or functional group diversity—exerts more significant influence on productivity remains controversial. Three primary challenges exist in alpine meadow research: First, alpine meadow species are dominated by rhizomatous or tufted grasses and sedges from Poaceae and Cyperaceae, requiring high specialization for species identification. Second, the core issue in functional group research depends on the selection of plant traits for classification, yet plant functional traits are not absolutely singular, leading to inconsistent functional group classifications. Third, because measuring belowground biomass in grassland communities is labor-intensive, many previous studies have used aboveground biomass alone as a proxy for productivity. However, grassland community belowground biomass often exceeds aboveground biomass by several times or more, and ignoring belowground biomass can substantially bias diversity-productivity relationships.

Lifeform, as the most fundamental basis for functional group classification, represents an indicator that reflects functional changes through external morphology. This classification is intuitive, accurate, and highly sensitive and responsive to grazing disturbance. Using lifeform as the basis for functional group classification can address challenges in specialized species identification and inconsistencies in purely functional trait-based classifications. Comparing the relationships of lifeform diversity and species diversity with grassland biomass holds important significance for clarifying the relationship between diversity and ecosystem productivity.

Alpine meadows serve as the primary grassland resource carrier on the Tibetan Plateau and play irreplaceable roles in regional and global ecological security and livestock production. Grazing intensity characteristics and seasonal dynamics represent the most important and unavoidable grazing disturbance patterns within a vegetation growth cycle. Richness, as an objective indicator that truly reflects diversity changes, has been widely used in studies of plant community composition changes. Therefore, investigating the relative importance of species richness versus lifeform richness in determining alpine meadow biomass under the combined effects of grazing intensity and season carries important model significance. This study selected a typical alpine meadow to conduct dynamic monitoring of plant richness and biomass changes across seasons, aiming to clarify the theoretical relationship between richness and biomass under grazing disturbance and determine the contribution capacity of lifeform richness to community productivity.

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1. Study Area Overview

The study area is located on the northeastern edge of the Tibetan Plateau, administratively within Zhaxi Xiulong Township, Tianzhu County, Gansu Province, at an elevation of 2958 m. The region has a mean annual temperature of -0.1°C and accumulated temperature >0°C of 1380°C. Annual precipitation is 400–480 mm, concentrated in June–September, accounting for 80% of annual rainfall. The soil type is alpine meadow soil. The study site experiences concurrent rainfall and heat, with both precipitation and temperature peaking in July–August. There is no absolute frost-free period, and the plant growing season lasts 120–140 days. Dominant species include *Elymus nutans*, *Stipa purpurea*, *Kobresia humilis*, and *Poa crymophila*.

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2. Plot Selection and Experimental Design

Based on systematic investigation of regional vegetation and local livestock carrying capacity, we calculated the moderate grazing intensity under year-round grazing conditions as 4.5–5.0 sheep units per hectare. We selected six plots with flat terrain, uniform vegetation, and consistent community structure, each covering 10 hm^2, with *Elymus nutans* and *Stipa purpurea* as dominant species. Gansu Alpine Fine-wool sheep of similar body weight were selected as experimental animals. Before the experiment, we conducted community surveys including species coverage and richness information. Year-round continuous grazing was implemented from 8:00 to 18:00 daily. As grazing intensity increased, soil moisture decreased and bulk density increased, causing significant changes in resource availability. This provided ideal conditions for comparative studies of the relationship between diversity (represented by richness) and biomass across spatial scales of different resource supplies and temporal scales before and after grazing.

Detailed information of study plots at the beginning of controlled grazing (mean±SD)

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3. Plant Community Survey

Plant community surveys were conducted in June (grassland green-up period), August (peak growing season), and October (grass withering period) using systematic random sampling. Each plot was regularly divided into 50 cm × 50 cm quadrats, with one quadrat randomly established in each subplot. Species richness was recorded as the number of species in each quadrat. Lifeform classification followed Whittaker' s plant lifeform classification system as revised by Gao and Chen, with species categorized into erect, rosette, and tufted types. Lifeform richness was represented by the number of lifeforms in each quadrat. Aboveground biomass was harvested by clipping vegetation at ground level, oven-dried at 65°C to constant weight. Belowground biomass was sampled using a 10 cm diameter soil corer at 0–10, 10–20, and 20–30 cm depths beside each quadrat, with three replicates per quadrat. Soil cores were washed through 0.5 mm mesh bags, and roots were oven-dried at 65°C and weighed to represent belowground biomass. A total of 270 quadrats were surveyed.

[Figure 1: see original paper] Environmental characteristics of study plots in 2014

Statistical Analysis Methods

1. Multiple Comparisons

Multiple comparisons of species richness, lifeform richness, and above- and below-ground biomass across different grazing intensities and seasons were performed using two-way ANOVA to test significance at = 0.05.

2. Community Lifeform Composition Ratio

We calculated the proportion of each lifeform by dividing the number of species of each lifeform by total species number in each quadrat. A plant matrix of lifeform composition and an environmental factor matrix of grazing intensity and season (quantified as 30, 90, and 150 for June, August, and October respectively) were established. Variance decomposition of grazing intensity and season effects on lifeform composition was performed with Monte Carlo permutation tests.

3. Linear Regression

Linear regression was used to fit relationships between above- and below-ground biomass and species/lifeform richness. The explanatory power of species richness and functional group richness for productivity was evaluated based on R^2 values.

4. Analysis Software

Data processing was conducted in Microsoft Excel 2013. Multiple comparisons and two-way ANOVA were performed in SPSS 19.0. Variance decomposition analysis was completed using CANOCO 5.0 for Windows.

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2. Results and Analysis

1. Changes in Species Richness and Lifeform Richness Under Grazing Disturbance

Species richness showed significant seasonal variation. Across different grazing intensities, low-intensity plots (Plot1, Plot2) exhibited significant changes, while high-intensity plots (Plot3, Plot4, Plot5, Plot6) showed no significant variation. A total of 45 species were surveyed. Species richness showed no significant differences with increasing grazing intensity in June and October, but decreased significantly with increasing intensity in August. Two-way ANOVA indicated that both grazing intensity ($F = 5.446$, $P = 0.000$) and season ($F = 5.561$, $P = 0.005$) significantly affected species richness, while their interaction did not ($F = 2.568$, $P = 0.030$).

Lifeform richness showed no regular pattern with grazing intensity or season. Two-way ANOVA showed that grazing intensity significantly affected lifeform richness ($F = 5.446$, $P = 0.000$), while season and their interaction did not.

Variation of species and lifeform richness under the impact of season and grazing intensity

Plant community species composition differed across grazing intensities and seasons. With increasing grazing intensity, the proportion of erect species decreased significantly while rosette species increased significantly in each season. As the season progressed, the proportion of tufted species decreased significantly during the peak growing season in August. Annual plants showed significantly decreased competitive advantage in both high- and low-intensity grazing areas in October. Variance decomposition indicated that grazing intensity contributed 6.20% to lifeform composition variation, reaching highly significant levels.

[Figure 2: see original paper] Lifeform composition ratio under grazing disturbance
Variance decomposition of grazing season and grazing intensity on lifeform composition

2. Aboveground Biomass Analysis

Aboveground biomass decreased significantly with increasing grazing intensity. Seasonal variation in aboveground biomass was significant only in low-intensity grazing plots (Plot1, Plot2), while no significant seasonal changes were observed in high-intensity plots (Plot3, Plot4, Plot5, Plot6). Two-way ANOVA further showed that both grazing intensity ($F = 30.461$, $P < 0.01$) and season ($F = 72.838$, $P < 0.01$) extremely significantly affected aboveground biomass.

3. Belowground Biomass Analysis

Belowground biomass showed significant seasonal variation only in the lowest grazing intensity plot (Plot1) and highest grazing intensity plot (Plot6), with no significant changes in other intensity plots. Two-way ANOVA indicated that season significantly affected belowground biomass ($F = 16.001$, $P < 0.01$), while grazing intensity showed no significant effect ($F = 0.346$, $P = 0.884$). Belowground biomass did not change significantly with increasing grazing intensity.

Variation of productivity under the impact of season and grazing intensity

3. Relationship Between Plant Richness and Biomass Before Grazing Disturbance

Before the grazing experiment (2012), both species richness and lifeform richness were significantly positively correlated with above- and below-ground biomass. Based on R^2 values, aboveground biomass was more strongly affected by richness changes than belowground biomass.

[Figure 3: see original paper] Relationships between richness and biomass before grazing disturbance (2012)

4. Relationships Between Richness and Biomass Under Different Seasonal Influences

Analysis of species richness-biomass relationships showed that aboveground biomass increased significantly with species richness in August, but not in June or October. Belowground biomass showed no significant relationship with species richness in any month. Lifeform richness analysis revealed that both above- and below-ground biomass increased significantly with lifeform richness in August, but not in other months. In June and October, neither species nor lifeform richness showed significant relationships with biomass.

[Figure 4: see original paper] Relationships between richness and biomass under different seasonal influences

5. Relationships Between Richness and Biomass Under Different Grazing Intensities

Analysis of species richness-biomass relationships showed that in low-intensity grazing plots, both above- and below-ground biomass increased significantly with species richness, while in high-intensity plots, no significant relationships existed. Across all grazing intensities, aboveground biomass increased significantly with lifeform richness. Belowground biomass increased significantly with lifeform richness only in low-intensity plots. In low-intensity plots, both species and lifeform richness were significantly positively correlated with above- and below-ground biomass, while in high-intensity plots, only lifeform richness was significantly positively correlated with aboveground biomass.

[Figure 5: see original paper] Relationships between lifeform richness and biomass in different plots

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3. Discussion

1. Impact of Grazing Disturbance on Species Richness, Lifeform Richness, and Biomass

As the primary ecosystem type on the Tibetan Plateau, alpine meadow biodiversity and productivity are greatly influenced by grazing disturbance. Plants exhibit different phenological periods and show seasonal differences in growth trends and responses to disturbance. This study found that plant richness and biomass responded to grazing intensity and season differently. Species richness decreased significantly with increasing grazing intensity in August, likely because severe grazing stress in high-intensity plots limited plant diversity expression. In June and low-intensity plots, higher environmental resource availability facilitated rapid growth of annual forbs, resulting in higher species richness. Lifeform richness was unaffected by season, as all lifeform types germinated rapidly during the green-up period. However, the proportion of tufted species decreased significantly in August, while erect and rosette species proportions increased, indicating that different lifeform plants adapt to seasonal changes through proportional adjustments.

Aboveground biomass decreased significantly with increasing grazing intensity because it is directly affected by grazing. Seasonal variation in aboveground biomass was significant only in low-intensity plots, suggesting that low-intensity grazing stimulates aboveground biomass growth. Belowground biomass showed no significant change with grazing intensity, consistent with findings that alpine *Kobresia* meadow root systems are extremely developed and less susceptible to grazing disturbance. This further demonstrates that belowground biomass responds slowly to short-term grazing disturbance.

2. Positive Linear Relationships Between Richness and Biomass During Peak Growing Season and Under Low Grazing Intensity

The relationship between plant richness and ecosystem productivity varies considerably across study areas, primarily because factors affecting richness and productivity differ. Grazing-induced environmental heterogeneity or community species composition differences can lead to different diversity-productivity patterns. This study found that in August—the season with the best water and heat resources during the year—and in low-intensity grazing plots, both species and lifeform richness showed positive linear relationships with aboveground biomass. When resource supply is adequate, increased richness facilitates differential resource utilization among species and lifeforms, maximizing resource use efficiency and enhancing ecosystem productivity, supporting the diversity-productivity hypothesis. The lack of relationship between belowground biomass and both species and lifeform richness in August and high-intensity plots indicates that when environmental resource limitations increase, differences in resource utilization among species cannot be fully expressed, particularly affecting the relationship between belowground biomass and species richness. Under stressful conditions, community species traits are constrained, and although species richness may increase, it may not lead to overall increases in root biomass across different plants.

3. Stronger Relationship Between Lifeform Richness and Biomass Than Species Richness Under Grazing Disturbance

Grazing disturbance significantly affects resource availability and plant resource utilization capacity, causing differential responses among community lifeforms and leading plants to first combine through morphological characteristics to adapt to environmental variation, thereby promoting ecosystem productivity. Before grazing, both species and lifeform richness were significantly positively correlated with above- and below-ground biomass. After grazing, aboveground biomass was positively correlated with species richness only in low-intensity plots, while aboveground biomass was positively correlated with lifeform richness across all grazing intensities. Belowground biomass was significantly correlated with both species and lifeform richness only in low-intensity plots.

Different species utilize environmental resources differently, and increased richness facilitates resource use by different species at different times and in different ways, maximizing resource use efficiency and increasing ecosystem productivity, supporting the diversity-productivity hypothesis. Belowground biomass responds slowly to disturbance. The impact of diversity on ecosystem production increases with increasing species diversity and lifeform differences. Lifeform richness more sensitively reflects community biomass size and positively affects aboveground biomass across all grazing intensities. This phenomenon can be explained by ecological redundancy or insurance: removing one or more species within a lifeform can be compensated by remaining species, making the removed species relatively redundant. However, removing an entire lifeform reduces community insurance, causing production function loss due to the disappearance of a specific species type.

4. Lifeform Richness Should Be Emphasized in Studies of Diversity-Productivity Relationships Under Short-Term Disturbance

Lifeform represents the morphological appearance, structure, and habits that plants develop to adapt to ecological environments. Under grazing disturbance, adjustments in plant community lifeforms determine whether communities can adapt to grazing habitats and maintain survival. Because different plant lifeforms employ different response strategies to grazing, they drive changes in species composition and replacement, forming the basis of community structure changes under different grazing intensities. This study found that lifeform richness consistently showed positive effects on aboveground biomass, more sensitively reflecting biomass changes.

Previous diversity-productivity studies have two main limitations: First, they examine diversity-productivity relationships at the species level, but alpine meadows dominated by tufted or rhizomatous sedges and grasses are extremely difficult to differentiate at the species level, limiting practical applicability. Second, they use functional group diversity based on species assemblages to simplify community complexity, but functional groups are classified based on physiological, life history, or other biological characteristics related to ecological processes and species behavior. The selection of biological characteristics depends on field surveys, and pure physiological functional differentiation under disturbance requires long time periods. Community lifeforms—plant external morphology—can respond to disturbance in relatively short timeframes. This study further demonstrates that increased lifeform richness allows differential utilization of spatial resources by differently shaped species, enabling all plants to grow actively and significantly affecting productivity. Lifeform richness shows great application potential under short-term disturbance. Morphological classification is more direct and accurate, can simplify community complexity from species-based to lifeform-based research units, and provides a theoretical approach to increase community productivity through enhanced lifeform richness. Due to its significant positive correlation with biomass, community primary productivity can be accurately and rapidly predicted at the lifeform richness level.

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Note: Figure translations are in progress. See original paper for figures.