Postprint: Topographic Controls on Soil Temperature and Moisture, Species Diversity, and Primary Productivity in Alpine Meadows

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Abstract

Mountains are the primary distribution areas of alpine meadows, where topographic variations cause differential distribution of soil temperature and moisture as well as species, thereby influencing the productive function of grassland ecosystems. To clarify the relationships between environmental factors (soil temperature and moisture) and species diversity (richness, abundance, evenness, dominance) with primary productivity in alpine meadow mountains, this study selected an alpine meadow mountain in the branch range of Maya Snow Mountain on the northeastern margin of the Qinghai-Tibet Plateau, choosing terraces, shady slopes, ridges, and sunny slopes across three altitude gradient segments, and surveyed the plant community composition and soil temperature and moisture in 189 quadrats. Linear regression methods were employed to analyze the relationships between soil temperature and moisture and species diversity with primary productivity. The results showed: (1) When the mountain alpine meadow was considered as an integrated study unit, primary productivity only increased significantly with species abundance (R2=0.07 P=0.01). (2) Slope aspect influenced the factors affecting primary productivity differently: primary productivity on shady slopes was positively linearly correlated with species richness; primary productivity on ridges was positively linearly correlated with soil moisture and also increased significantly with species richness; primary productivity on sunny slopes was positively linearly correlated with species abundance; primary productivity on terraces increased significantly with evenness and decreased significantly with dominance. (3) Only in the low-altitude area (2860-2910 m) did primary productivity increase significantly with increases in both species abundance and richness. In summary, the relationships between soil temperature and moisture and species diversity with primary productivity in mountain alpine meadows were more strongly influenced by slope aspect than by altitude, and species diversity had a greater impact on primary productivity

than soil temperature and moisture. It is recommended that the effects of slope aspect on plant diversity and primary productivity be given priority consideration in the production and ecological management of mountain alpine meadow ecosystems.

Full Text

Preamble

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Relationships Between Soil Moisture and Temperature, Plant Species Diversity, and Primary Productivity in an Alpine Meadow Considering Topographic Factors

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Abstract

Alpine meadows are predominantly distributed in mountainous regions. Topographic variation induces differential distribution of soil temperature and moisture as well as plant species, thereby influencing ecosystem primary production. To elucidate the relationships between environmental factors (soil moisture and temperature), species diversity (richness, abundance, evenness, and dominance), and primary productivity in alpine meadow ecosystems, we investigated plant community structure and soil moisture and temperature at 189 sampling sites across lowland (bottom land), shady aspect, ridge, and sunny aspect along three elevation gradients on a hillside in the Qilian Mountains, Tianzhu County, on the northeastern edge of the Qinghai-Tibet Plateau. Linear regression analysis was employed to examine the relationships among these variables.

When the entire hillside was treated as a single unit, primary productivity increased significantly only with increasing species abundance (R^2 = 0.07, P = 0.01). However, distinct patterns emerged across different slope aspects: on the shady aspect, primary productivity showed a positive linear correlation with species richness; on the ridge, primary productivity exhibited a positive linear correlation with soil moisture, which itself increased significantly with species richness; on the sunny aspect, primary productivity was positively linearly correlated with species abundance; and on bottom land, primary productivity was positively linearly correlated with species evenness. In low-elevation plots (2860–

2910 m), primary productivity increased significantly with both species abundance and richness.

We conclude that slope aspect exerted a greater influence than elevation on the relationships between soil moisture, temperature, species diversity, and primary productivity in this alpine meadow system, and that species diversity had a stronger effect on primary productivity than soil temperature and moisture. We recommend that slope aspect should be the primary consideration—rather than elevation—in grassland production and ecological management assessments for alpine meadow ecosystems.

Keywords: alpine meadow; mountains; soil temperature; soil moisture; species diversity; primary productivity

1. Introduction

Primary productivity in ecosystems represents a comprehensive response to soil hydrothermal conditions and other environmental factors. Mountains constitute the typical terrain of the Qinghai-Tibet Plateau, and as special habitat islands, mountain topography determines the redistribution of water and heat resources while influencing species diversity. Alpine meadows, the predominant grassland type on the Qinghai-Tibet Plateau, are mainly distributed across mountainous regions. Topography serves as a critical abiotic factor driving variation in species diversity and soil hydrothermal resources, making the relationship among grassland species diversity, soil water/heat, and ecosystem function a focal topic in contemporary ecological research.

Primary productivity is widely recognized as a key indicator reflecting ecosystem service functions. Species diversity, as a comprehensive metric encompassing richness, dominance, and heterogeneity measurements, represents different community composition structures that have formed through long-term evolutionary processes. Plant communities dynamically respond to environmental factors, with water and heat resource allocation becoming the primary mechanism influencing plant diversity and subsequent productivity changes. Both community species composition and soil factors jointly influence these patterns.

Slope aspect and elevation are the most important topographic factors in alpine meadows, directly affecting the spatial redistribution of solar radiation and precipitation, leading to differential distribution of soil moisture and temperature. Previous studies on productivity-diversity relationships have typically employed one of three approaches: (1) large geographic scales and organizational levels to eliminate topographic interference, thereby ignoring specific variation in soil hydrothermal conditions and community diversity within small-scale mountain units; (2) small-scale homogeneous habitats and artificial communities for simulation studies, neglecting the influence of strong spatial heterogeneity at larger scales on relationships among soil water/heat, diversity, and productivity; or (3) mountain studies focusing only on different aspects or elevations at the same spatial level, with sampling conducted across different mountains, preventing systematic investigation of the mountain system as a whole across spatial levels or aspect and elevation gradients. These approaches have yielded inconsistent results with limited comparability.

Although small-scale mountain ecological studies have identified topography as the main factor influencing heterogeneous distribution of soil temperature and moisture, with slope aspect being the dominant factor driving differences in species diversity and soil water content, it remains unclear which component of soil temperature/moisture and species diversity more strongly influences productivity at both the whole-mountain level and local aspect/elevation levels. Small-scale mountains serve as the most basic topographic units for managing alpine meadow ecosystems, eliminating climate differences from geographic variation and providing ideal systems for studying relationships among water/heat resources, species diversity, and productivity under the combined effects of slope aspect and elevation. Therefore, this study selected a representative small-scale alpine meadow hillside on the Mayaxue Mountain branch at the eastern edge of the Qilian Mountains on the northeastern edge of the Qinghai-Tibet Plateau, excluded interference from geographic factors, and focused solely on the two-dimensional variables of aspect and elevation to investigate relationships among soil temperature/moisture, species diversity, and primary productivity. We examined which component—soil temperature/moisture or biodiversity—more strongly influences primary productivity at both the entire branch hillside level and across aspect and elevation gradients, aiming to provide scientific evidence for large-scale mountain ecological studies and rational utilization of small-scale alpine meadows.

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2. Materials and Methods

2.1 Study Area

This study was conducted on a branch hillside of the Mayaxue Mountain on the eastern edge of the Qilian Mountains in Tianzhu Tibetan Autonomous County, Gansu Province, on the northeastern edge of the Qinghai-Tibet Plateau. The study area extended from 2850 to 3020 m in elevation along the ridge line, with geographic coordinates of 37°09 -37°14 N, 102°40 -102°47 E. The average slope was 8–10°, with a total grassland area of approximately 150 hm^2. The region has a typical alpine meadow climate, with mean annual precipitation of 416 mm (concentrated in July-September, accounting for 80% of annual rainfall), mean annual temperature of -0.5°C, annual potential evaporation of 1592 mm, >0°C accumulated temperature of 1380°C, and a frost-free period of 120–140 days. The soil type is alpine meadow soil with a thickness of 40–50 cm. While all vegetation types belong to the alpine meadow category, distinct community differences exist due to microhabitat variation: the shady aspect is dominated by

Polygonum viviparum, the ridge by *Kobresia capillifolia*, the terrace by *Elymus nutans* and *Artemisia smithii*, and the sunny aspect by *Stipa purpurea* and *Koeleria cristata*.

2.2 Experimental Design

We employed a large-sample systematic sampling approach, selecting the entire alpine meadow branch hillside with consistent slope and grazing intensity to eliminate interference from macroclimate, grazing, and slope variation. The hillside was divided into four aspects: shady aspect (SHA), ridge (RI), sunny aspect (SUA), and bottom land (BL). The elevation gradient was divided into three levels: low elevation (LO, 2860–2910 m), medium elevation (ME, 2910–2960 m), and high elevation (HI, 2960–3020 m). Beginning at the base, we established transects perpendicular to the ridge line. Within each transect, we set up 0.5 m × 0.5 m quadrats at upper and lower positions on both shady and sunny aspects, with parallel quadrats on terraces and along the ridge, totaling 189 sampling sites. We surveyed plant community structure in all quadrats and measured soil temperature and moisture.

2.3 Plant Community Survey and Soil Measurements

Vegetation surveys were conducted during the peak growth period in mid-July. Using systematic sampling, we recorded: species richness (number of species per 0.25 m^2 quadrat), species coverage (visual estimation of each species' coverage), and species frequency (randomly tossing a 0.25 m^2 circular quadrat near each plot to record species presence). Species abundance was represented by individual counts, with tussock-type grasses counted as one plant if inseparable, and rhizomatous grasses counted as one plant per rooted stem. Aboveground biomass was harvested by clipping all plants at ground level within each quadrat, placed in envelopes, oven-dried at 65°C to constant weight, and weighed to represent primary productivity.

Species importance value was calculated as the average of relative coverage and relative frequency. Species evenness (Ev) and Berger-Parker dominance index were computed using maximum value standardization. Soil temperature and moisture were measured at 0–10, 10–20, and 20–30 cm depths using a TSZ-IIW soil moisture-temperature meter, with three measurements averaged for each depth and then averaged across depths (0–30 cm) for each quadrat. GPS recorded latitude, longitude, and elevation.

2.4 Data Analysis

We first conducted multiple comparison analysis (LSD) of species richness, soil temperature, and moisture across different aspects and elevations. Linear regression analyzed relationships among soil temperature/moisture, species diversity, and primary productivity. To exclude mutual interference between soil temperature/moisture and species diversity, we performed partial correlation analyses: (1) controlling for soil temperature/moisture to examine species diversity-productivity relationships, and (2) controlling for species diversity to examine soil temperature/moisture-productivity relationships. Partial correlation coefficients (R^2) quantified the relative contributions. All statistical analyses used SPSS 19.0 with significance set at P = 0.05.

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3. Results

3.1 Variation in Soil Temperature, Moisture, Species Diversity, and Primary Productivity

Survey results showed that soil temperature was highest on the medium-elevation sunny aspect, while soil moisture peaked on the high-elevation shady aspect. Species richness was highest on the medium-elevation shady aspect, abundance on the high-elevation ridge, evenness on the low-elevation sunny aspect, and dominance on the high-elevation shady aspect. Primary productivity was highest on the medium-elevation shady aspect. Soil temperature and moisture showed strong spatial variability: on shady aspects, temperature was low with small variation coefficients while moisture was high with large variation; on sunny aspects, moisture was low with small variation while temperature was high with large variation. Ridge and terrace soils had intermediate temperature and moisture levels, but terraces showed significant negative correlation between temperature and moisture ($R^2 = 0.19$, $P = 0.00$), while ridge soils showed significant positive correlation ($R^2 = 0.72$, $P = 0.00$) .

3.2 Relationships at the Whole-Hillside Scale

Based on data from all 189 quadrats, linear regression models revealed that primary productivity increased significantly only with species abundance ($R^2 = 0.07$, $P = 0.01$) when the entire hillside was treated as a single unit. No other indices showed significant relationships with primary productivity [Figure 3: see original paper].

3.3 Relationships Across Different Slope Aspects

On the shady aspect, primary productivity increased significantly with species richness ($R^2 = 0.13$, $P = 0.00$). On the ridge, primary productivity increased significantly with both soil moisture ($R^2 = 0.12$, $P = 0.02$) and species richness ($R^2 = 0.12$, $P = 0.04$). On the sunny aspect, primary productivity increased significantly with species abundance ($R^2 = 0.12$, $P = 0.04$). On terraces, primary productivity increased significantly with evenness ($R^2 = 0.28$, $P = 0.00$) and decreased significantly with dominance ($R^2 = 0.49$, $P = 0.03$). No other diversity indices showed significant relationships, and no other aspects showed significant correlations with soil temperature or moisture. Partial correlation R^2 values indicated that species diversity had greater influence on community primary productivity than soil factors [FIGURE:4, FIGURE:5, TABLE:2].

3.4 Relationships Across Different Elevation Gradients

At low elevations, community primary productivity increased significantly with species abundance (R^2 = 0.19, P = 0.02) and richness (R^2 = 0.31, P = 0.00). No significant relationships were observed between species diversity indices and primary productivity at medium or high elevations, nor between soil temperature/moisture and primary productivity across any elevation gradient. Partial correlation R^2 values showed that, except for the strong influence of species abundance and richness at low elevations, soil temperature/moisture and species diversity had limited impact on primary productivity at other elevations [FIGURE:6, FIGURE:7].

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4. Discussion and Conclusions

4.1 Species Abundance as the Primary Driver of Primary Productivity at the Hillside Scale

Treating the alpine meadow hillside as an integrated unit, we found that primary productivity increased significantly only with species abundance, despite strong spatial variability in soil temperature and moisture across aspects and elevations that showed no significant direct relationships with productivity. This contrasts with large-scale studies emphasizing environmental factors as stronger drivers of productivity than species diversity. The discrepancy likely stems from differences in research scale: across large environmental gradients, hydrothermal conditions become decisive factors, whereas at small hillside scales, although topography induces soil water/heat variation, species diversity changes are more pronounced and community composition adjustments more active. Species can exploit minor environmental heterogeneity to survive, and internal community adjustments allow different plants to access required nutrients, indicating that primary productivity in small-scale alpine meadows is more strongly regulated by biotic community processes than abiotic factors. Additionally, previous studies often sampled along roads or railways across large geographic regions without accounting for grazing intensity differences, which may have confounded results. Our small-scale approach avoids these issues.

4.2 Slope Aspect Exerts Greater Influence Than Elevation

In natural ecosystems, both species diversity and productivity are strongly influenced by abiotic factors, particularly soil temperature and moisture. Previous research identified slope aspect-induced variation in soil water content as the primary factor limiting plant growth and distribution. While both soil hydrothermal conditions and species diversity positively affected productivity across aspects, elevation effects were limited: only low-elevation productivity increased with species abundance and richness. The elevation gradient spanned only 170 m, with temperature lapse rate of 0.5-0.7°C per 100 m, causing minimal impact on soil hydrothermal conditions and community structure compared to aspect. Slope aspect created substantial differences in water/heat supply and species diversity distribution. We recommend that hillside-scale alpine meadow ecosystem management and restoration should prioritize aspect-related effects on plant diversity and productivity over elevation.

4.3 Aspect-Specific Drivers of Primary Productivity

Soil hydrothermal conditions and species diversity are key factors influencing alpine meadow primary productivity. Previous diversity-productivity research often used species richness as the sole diversity metric, reporting linear, hump-shaped, or neutral relationships, with water/heat supply considered a major cause of variation. Our results show that different diversity components reflect differences in community composition, function, and dynamics, with their relationships to productivity varying by water/heat availability. On the shady aspect, with adequate water supply, increased species richness enhanced temporal resource use efficiency and productivity. The ridge, with its special geographic position and limited water retention, showed productivity primarily driven by soil moisture. On the sunny aspect, high temperatures and limited water prevented high species coexistence, so productivity depended on species abundance. On terraces, with abundant nutrients and minimal heterogeneity, productivity increased with evenness but decreased with dominance, as more uniform species distribution enhanced community productivity when dominant species' control was reduced. These findings align with controlled homogeneous grassland experiments and highlight the importance of considering specific habitat types and spatial scales in diversity-productivity studies.

References

[1] [References section appears to be truncated in the original text and would be preserved exactly as provided in a complete translation]

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