Effects of Topography on Aboveground Biomass Variation in Understory Shrub-Herb Layers of Temperate Dense Forests: A Case Study from Northeast China Tiger and Leopard National Park (Postprint)

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Abstract

To investigate the effects of terrain on shrub and herb layer biomass, this study employed a nested design to survey 138 understory sample plots comprising 1,685 plant quadrats in Northeast Tiger and Leopard National Park. The influence of terrain on understory shrub and herb layer plant biomass was analyzed through nested analysis of variance and ordinal logistic regression models. The results indicated that: (1) Among different slope positions, valley shrub and herb biomass was greater than upper slope, which was greater than lower slope ($P < 0.01$); among different slope aspects, shady slope shrub and herb layer biomass was lower than sunny slope and flat ground ($P < 0.01$), with no significant difference between the latter two; among different slope gradients, steep slope shrub and herb layer biomass was higher than moderate slope, which was higher than gentle slope ($P < 0.01$). (2) The interaction effect between slope position and slope aspect was significant; lower slope flat ground, upper slope flat ground, upper slope sunny slope, and all slope positions in valley had the highest shrub and herb biomass, with no significant differences among lower slope shady slope, lower slope sunny slope, and upper slope shady slope. (3) Under current conditions in the study area, logistic regression results showed that shrub and herb biomass varied across different combinations of elevation, slope position, and slope aspect/slope gradient. Slope position, slope aspect, and slope gradient had significant effects on understory shrub and herb biomass; among the three slope position levels, valley bottom was highest while lower slope was lowest; among the three slope gradient levels, steep slope was highest while gentle slope was lowest; and among different slope aspects, shady slope was lowest. (4) Under realistic conditions without excluding human disturbance and forest grazing, valley and steep slope areas had the highest probability of high shrub and herb biomass production. This study can provide important reference for accurately estimating the carrying capacity of understory shrub and herb layer plants for tiger and leopard prey populations in Northeast Tiger and Leopard National Park, thereby offering scientific basis for the conservation and management of endangered tigers and leopards.

Full Text

Impacts of Topographic Factors on Spatial Variability of Temperate Closed Forest Understory Biomass: A Case Study of Northeast China Tiger and Leopard National Park

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Abstract: To investigate the impacts of topography on understory biomass, this study employed a nested design to survey 138 plots comprising 1,685 plant quadrats in Northeast China Tiger and Leopard National Park. Nested analysis of variance and ordinal logistic regression were used to analyze topographic effects on understory shrub and herb biomass. Results showed: (1) Among slope positions, valley understory biomass was significantly greater than upper slopes, which in turn exceeded lower slopes ($P < 0.01$). For slope aspects, shaded slopes had lower biomass than sunny slopes and flat terrain ($P < 0.01$), with no significant difference between the latter two. Across slope gradients, steep slopes supported higher biomass than moderate slopes, which exceeded gentle slopes ($P < 0.01$). (2) The interaction between slope position and aspect was significant. The highest biomass occurred on flat lower slopes, flat upper slopes, sunny upper slopes, and all valley positions. The lowest biomass occurred on shaded lower slopes, sunny lower slopes, and shaded upper slopes, which did not differ significantly from each other. (3) Logistic regression revealed that understory biomass varied across different combinations of elevation, slope position, and aspect. Slope position, aspect, and gradient all significantly influenced biomass: among three slope position classes, valleys were highest and lower slopes lowest; among three slope gradient classes, steep slopes were highest and gentle slopes lowest; among aspects, shaded slopes were lowest. (4) Under current conditions with human disturbance and forest grazing, valleys and steep slope areas showed the highest probability of high understory biomass. This study provides crucial reference data for accurately estimating the carrying capacity of understory vegetation for ungulate prey populations, thereby informing conservation and management of endangered tigers and leopards.

Keywords: topography, understory, forage resource, biomass, logistic regression

In Northeast China Tiger and Leopard National Park and adjacent areas, large and medium-sized ungulates such as sika deer (*Cervus nippon*), roe deer (*Capreolus pygargus*), and wild boar (*Sus scrofa*) constitute the primary prey for Amur tigers (*Panthera tigris altaica*) and Amur leopards (*P. pardus orientalis*) (Kerley et al., 2015; Yang et al., 2018; Wang et al., 2020). These ungulates predominantly feed on understory shrub and herb layer vegetation (Massei et al., 1996; Baskin & Danell, 2003; Gordon & Prins, 2008; Barančeková et al., 2010; Wang et al., 2019a). Consequently, understory plant biomass represents a critical factor influencing ecosystem carrying capacity for herbivores (Whittaker & Likens, 1973; Gilliam & Roberts, 2003). During early spring, sparse canopy foliage allows abundant light to reach the forest floor, enabling rapid understory growth. However, as the canopy closes, understory light availability decreases substantially (Wang et al., 2006), particularly after full canopy closure when understory biomass accumulation slows (Jolly et al., 2004). At this stage, the relative importance of topographic factors for understory productivity becomes increasingly pronounced (Gracia et al., 2007).

Complex terrain creates diverse microenvironments that influence local microclimate and soil conditions, thereby affecting key growth factors including light, temperature, water, and nutrients (Gong, 2016; Shen et al., 2017; Li et al., 2019; Sun et al., 2020; Li & Gong, 2021). Topographic factors such as elevation, slope position, gradient, and aspect regulate these ecological factors, shaping the spatially heterogeneous distribution of understory plant resources (Gong, 2016). However, few studies have examined topographic effects on forest biomass in the national park region. In the Jingouling Forest Farm of Changbai Mountains, forest aboveground biomass varied significantly with elevation and slope gradient but not with aspect (Jiang, 2011). Elevation, slope gradient, and aspect significantly influenced spatial heterogeneity of forest biomass in the Greater Khingan Mountains (Li, 2010). In the Lesser Khingan Mountains, slope position and aspect were important topographic factors affecting tree and shrub layer biomass, with biomass first increasing then decreasing with slope position, and decreasing from shaded to semi-shaded to semi-sunny to sunny slopes and flat terrain (Wang, 2013). In Maoershan, Heilongjiang, forest biomass correlated significantly with elevation and slope gradient but not with aspect (Wang et al., 2010). These findings demonstrate the complex effects of topographic factors on local forest biomass. While numerous studies have addressed forest biomass heterogeneity (Gordon & Prins, 2008), research specifically targeting understory biomass remains limited (de Castilho et al., 2006; Nie et al., 2019). Investigating topographic influences on understory biomass is fundamental for understanding its spatial variation patterns and for assessing ecosystem herbivore carrying capacity.

This study focuses on Northeast China Tiger and Leopard National Park, targeting the closed forest understory vegetation that constitutes the primary food source for large ungulates. Using nested ANOVA and ordinal logistic regression, we analyzed understory biomass in relation to elevation, slope position, aspect, and gradient. Our objectives were to: (1) characterize how topographic factors influence spatial variation in closed forest understory biomass, and (2) predict terrain conditions associated with high-yield biomass areas. The findings will provide firsthand data for accurately estimating ungulate carrying capacity and inform tiger and leopard conservation management.

1.1 Study Area Description

The study area lies in the eastern portion of Northeast China Tiger and Leopard National Park (42°30 –44°10 N, 129°10 –131°20 E), representing the primary distribution and priority protection zone for Amur tigers and leopards in China (Hebblewhite et al., 2014; Wang et al., 2016; Feng et al., 2017). The region experiences a semi-humid continental monsoon climate, with mean temperatures of -15 °C in January and 20 °C in July. Annual precipitation ranges from 365.0 to 842.9 mm (30-year record), with concurrent rainfall and heat, and deep winter snowpack. The mountainous and hilly terrain varies in elevation from 2 to 1,486 m, with major rivers including the Hunchun, Tumen, Gaya, and Suifen. The landscape features diverse landforms: along the Hunchun River valley, terrain is flat with low elevation and gentle slopes, while deeper mountainous areas show higher elevations and steeper, more prominent ridges. Zonal soils are dark brown forest soils, and zonal vegetation is broadleaf-Korean pine (*Pinus koraiensis*) forest. However, economic activities and logging have largely replaced these with secondary forests at various successional stages, including broadleaf mixed forests, Mongolian oak (*Quercus mongolica*) stands, and poplar (*Populus davidiana*) forests (Zhou & Li, 1964; Wu, 1980).

Understory shrubs are dominated by *Rhododendron*, *Philadelphus*, *Deutzia*, *Schisandra*, *Rubus*, *Corylus*, and *Lonicera*, while herbaceous species include *Carex*, *Melica*, *Potentilla*, *Thalictrum*, *Astilbe*, *Viola*, *Rubia*, *Filipendula*, *Isodon*, *Parasenecio*, *Vicia*, *Artemisia*, and *Pteridium* (Wang et al., 2023). The fauna includes Amur tigers, Amur leopards, sika deer, roe deer, and wild boar (Xiao et al., 2014; Zhang et al., 2014; Wang et al., 2016). Key forage plants for ungulates include *Acer tegmentosum*, *Abies nephrolepis*, *Tilia amurensis*, *Betula platyphylla*, *Acer pictum* subsp. *mono*, *Corylus mandshurica*, *Sorbaria sorbifolia*, *Dryopteris crassirhizoma*, and *Carex* spp. (Wang, 2019).

1.2 Data Collection

During the 2015–2016 growing seasons (June–August), we randomly selected 140 plots for vegetation surveys. At each plot center, we established four 50-m transects in the cardinal directions (north, east, west, south). Along each transect, we selected four random points and established a 1 m × 1 m quadrat at each point. We harvested aboveground biomass of herbaceous plants (excluding mosses) and current-year twigs and leaves of trees and shrubs below 2.2 m height, then air-dried and transported samples to the laboratory.

Within each plot, we recorded elevation at the center using a GPS unit (GARMIN Rino 530HCx, USA) and measured slope aspect (0–360°) with a compass, classifying aspects as shaded (0–135° and 315–360°), sunny (135–315°) (Zhang et al., 2016), or flat. Plots were divided into high (>500 m) and low ($ 500*m*)*elevationcategories*.*Alongeachtransect*, *werecordedslopepositionforthefourquadratsasupperslope*, gentle (5°–25°), or steep (>25°). Due to hazardous terrain such as cliffs, we surveyed 496 transects with 1,948 quadrats. Using a canopy analyzer (WinScanopy), we measured canopy closure. Open habitats (closure <0.7) such as gaps, edges, and riversides (263 quadrats) were excluded as they introduced additional light and moisture effects beyond the scope of this study. The final dataset comprised 1,685 quadrats from 138 closed-canopy plots (closure 0.7–0.9) (Wang et al., 2019a).

1.3.1 Nested Analysis of Variance

Although the 1,685 understory quadrats were largely independent with environmental data recorded at the quadrat level, most environmental factors were nested within the 138 plots. To avoid inflated degrees of freedom from potential spatial autocorrelation, we used linear mixed models with plot as a nested factor, focusing on topographic effects. Using elevation, slope position, aspect, and gradient as categorical predictors and total understory biomass as the response variable, we performed nested multivariate univariate ANOVA followed by Tukey's HSD tests. Prior to analysis, we tested for significant differences in total understory biomass across survey years and months; results showed no significant temporal variation, permitting subsequent analyses. All statistical computations were conducted in R (v4.2.2) using the multcomp, lattice, lme4, and lsmeans packages (R Core Team, 2021).

1.3.2 Ordinal Logistic Regression Procedure

For variables with more than two categories, we employed ordinal logistic regression to predict understory biomass probability across topographic combinations. This model sequentially partitions the response variable into three levels, establishing a three-category logistic regression model (Zhang, 2002). The formulas are as follows (Equations 1–7):

$$
\begin{aligned}
\text{odds} &= \frac{P}{1-P} \\
\ln(\text{odds}) &= \ln\left[\frac{P}{1-P}\right] \\
\text{logit}(P_1) &= \alpha_1 - (\beta_{1x}1 + \cdots + \beta_{nx}n) = \ln\left[\frac{P_1}{1-P_1}\right] \\
\text{logit}(P_1+P_2) &= \alpha_2 - (\beta_{1x}1 + \cdots + \beta_{nx}n) = \ln\left[\frac{P_1+P_2}{1-P_1-P_2}\right] = \ln\left[\frac{P_1+P_2}{P_3}\right] \\
P_1 &= \frac{e^{\text{logit}(P_1)}}{1+e^{\text{logit}(P_1)}} = \frac{\exp[\alpha_1 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]}{1+\exp[\alpha_1 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]} \\
P_2 &= (P_1+P_2) - P_1 = \frac{\exp[\alpha_2 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]}{1+\exp[\alpha_2 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]} - \frac{\exp[\alpha_1 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]}{1+\exp[\alpha_1 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]} \\
P_3 &= 1 - (P_1+P_2) = 1 - \frac{\exp[\alpha_2 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]}{1+\exp[\alpha_2 - (\beta_{1x}1 + \cdots + \beta_{nx}n)]}
\end{aligned}
$$

Where: P represents event probability (0–1), with P_1, P_2, and P_3 denoting probabilities for the three response categories; x represents independent variables ($x_1 \ldots x$); α represents constants; and β represents variable coefficients.

1.3.3 Ordinal Logistic Regression Analysis

To predict understory biomass, we combined variables from the ANOVA analysis. Some combinations were nonexistent or had extremely low sample sizes (e.g., flat/gentle, flat/steep, valley/steep had only one quadrat). Therefore, we merged aspect and gradient into five categories: shaded-gentle, sunny-gentle, shaded-steep, sunny-steep, and flat, while combining valley steep (both aspects) with valley flat. These categorical variables were converted to dummy variables before regression (Table 1).

We classified understory biomass into three levels: low (\$ $20g{\cdot}m^{\text{\{-2\}}), medium(20–40g \cdot m$ {-2}), $and high(> 40g \cdot m$^{-2}\$). Using ordinal logistic regression with elevation, slope position, and aspect-gradient as predictors, we calculated probabilities for each biomass level using IBM SPSS Statistics v20.0 (SPSS Company, Chicago, USA).

2.1 Species Composition of Closed Forest Understory

Our survey identified 172 species across 58 families and 121 genera, including 44 tree species (seedlings and saplings), 23 shrubs, 7 woody vines, 3 grasses, 5 sedges, 83 forbs, and 7 ferns. Rosaceae and Caprifoliaceae dominated the shrub layer, while Liliaceae, Lamiaceae, Fabaceae, Violaceae, Asteraceae, Ranunculaceae, Apiaceae, and Cyperaceae were most abundant among herbaceous plants (Table 2).

At high elevations (>500 m) on upper slopes, forests were primarily mixed coniferous-broadleaf stands dominated by Korean pine and spruce-fir, or deciduous broadleaf mixtures of birch, poplar, linden, and oak. Understory shrubs included *Corylus heterophylla*, *Spiraea fritschiana*, and *Eleutherococcus senticosus* (cover 10–20%), while herbs such as *Thalictrum ichangense* var. *coreanum*, *Vicia cracca*, and *Heracleum dissectum* dominated (cover 30–45%). Low-elevation (<500 m) upper slopes supported pure Mongolian oak stands or mixed forests with oak, maple, ash, and linden. Shrubs included *Rhododendron schlippenbachii*, *R. dauricum*, *Philadelphus tenuifolius*, *Deutzia parviflora* var. *amurensis*, and *Lespedeza bicolor* (cover 20–30%). Herbaceous species comprised *Melampyrum roseum*, *Convallaria majalis*, *Astilbe chinensis*, *Parasenecio* species, *Actaea simplex*, and various *Carex* species (cover 20–30%).

Lower slopes and valleys above 500 m featured coniferous-broadleaf mixed forests, while those below 500 m were dominated by mixed hardwoods including *Larix olgensis*, *Abies nephrolepis*, *Alnus hirsuta*, *Fraxinus mandshurica*, *Ulmus pumila*, and maple species. Shrubs such as *Viburnum opulus* subsp. *calvescens*, *Sorbaria sorbifolia*, and *Syringa villosa* subsp. *wolfii* were common (cover 30–40%). Herbaceous vegetation included *Patrinia scabiosifolia*, *Impatiens noli-tangere*, *Adenophora divaricata*, *Ligularia fischeri*, *Caltha palustris*, *Ranunculus japonicus*, *Aconitum carmichaelii*, *Filipendula palmata*, *Urtica angustifolia*, *Hylomecon japonica*, *Calamagrostis epigeios*, various *Carex* species, and ferns (cover 30–45%).

2.2.1 Baseline Understory Biomass

Analysis of 1,685 closed-canopy quadrats revealed shrub layer biomass of 12.26 ± 0.30 $g \cdot m^{-2}$ (mean ± SE), with first quartile (Q1) = 3.25 $g \cdot m^{-2}$, median (Q2) = 9.11 $g \cdot m^{-2}$, and third quartile (Q3) = 17.51 $g \cdot m^{-2}$. Herbaceous layer biomass was 17.84 ± 0.39 $g \cdot m^{-2}$ (Q1 = 5.44 $g \cdot m^{-2}$, Q2 = 13.46 $g \cdot m^{-2}$, Q3 = 25.87 $g \cdot m^{-2}$). Total understory aboveground biomass was 30.15 ± 0.44 $g \cdot m^{-2}$ (Q1 = 16.50 $g \cdot m^{-2}$, Q2 = 26.45 $g \cdot m^{-2}$, Q3 = 40.40 $g \cdot m^{-2}$) (Figure 1 [Figure 1: see original paper]).

2.2.2 Topographic Effects on Total Understory Biomass

Nested ANOVA using linear mixed models (Table 3) showed that slope position, aspect, and gradient significantly affected understory biomass ($P < 0.01$), while elevation had no significant effect ($P > 0.05$). The interaction between slope position and aspect was significant; other interactions were not. Tukey post-hoc comparisons revealed: (1) Significant differences among three slope position classes, with biomass ranking: valley > upper slope > lower slope (Figure 2 [Figure 2: see original paper]A); (2) Shaded slopes had significantly lower biomass than sunny slopes and flat terrain, which did not differ significantly (Figure 2A); (3) Significant differences among three gradient classes, with biomass ranking: steep > moderate > gentle slopes (Figure 2A); (4) The position × aspect interaction (Figure 2B) showed that flat lower slopes, flat upper slopes, sunny upper slopes, and all valley positions had the highest biomass (no significant differences among them), while shaded lower slopes, sunny lower slopes, and shaded upper slopes had the lowest biomass (no significant differences among them).

2.2.3 Probability of Understory Biomass Across Topographic Combinations

Logistic regression results indicated good model fit, passing the parallel lines test (P = 0.72). All three categorical variables—elevation, slope position, and aspect-gradient—were significant ($P < 0.05$) and included in the final model (Table 4). Odds ratios showed that low-elevation understory biomass was 0.76 times that of high-elevation areas; lower slopes were 0.47 times and upper slopes 0.69 times that of valleys. Using sunny-steep slopes as reference, shaded-gentle slopes had 0.35 times the biomass, sunny-gentle slopes 0.49 times, shaded-steep slopes 0.66 times, and flat slopes 0.63 times (Table 4).

Based on these results, the link functions were derived as:

$$\begin{aligned}\text{Link1} &= -1.82 - (\alpha_{\text{elevation}} + \beta_{\text{position}} + \gamma_{\text{aspect-gradient}})\\ \text{Link2} &= -0.03 - (\alpha_{\text{elevation}} + \beta_{\text{position}} + \gamma_{\text{aspect-gradient}})\end{aligned}$$

Where α, β, and γ represent coefficients for elevation, slope position, and aspect-gradient, respectively. Variable coding rules: (1) Elevation is binary: α = -0.27 for low elevation (coded 1), 0 for high elevation (coded 2); (2) Slope position is three-level: select corresponding β coefficient from Table 5 based on position (1 = lower, 2 = upper, 3 = valley); (3) Aspect-gradient is five-level: select corresponding γ coefficient based on category (1 = shaded-gentle, 2 = sunny-gentle, 3 = shaded-steep, 4 = flat, 5 = sunny-steep). Each factor has one reference category with coefficient set to 0 (Zhang, 2002). After calculating link functions, values are substituted into prediction formulas.

3.1 Topographic Impacts on Understory Biomass

Total understory aboveground biomass in closed forests was approximately 0.30 $\text{t}\cdot\text{hm}^{-2}$, consistent with Liu et al. (2019) who reported 0.08–0.69 $\text{t}\cdot\text{hm}^{-2}$ (mean 0.30 $\text{t}\cdot\text{hm}^{-2}$) in Jigongshan, Henan Province. Herbaceous biomass (0.18 $\text{t}\cdot\text{hm}^{-2}$) was lower than the 0.49 $\text{t}\cdot\text{hm}^{-2}$ average for 40–60°N forests and 0.42 $\text{t}\cdot\text{hm}^{-2}$ for 30–40°N latitudes (DeAngelis et al., 1981; Gilliam, 2003), likely due to differences in community composition and the significant influence of latitude, mean annual temperature, and precipitation on understory biomass at broad scales (Jin et al., 2022).

At our finer study scale, understory biomass showed significant spatial variation, with elevation, slope position, aspect, and gradient all exerting strong effects (Zhang et al., 2023). High-elevation biomass exceeded low-elevation by approximately 10%, possibly due to greater human disturbance (cattle grazing, ginseng cultivation, frog farming, non-timber product collection) at lower elevations, though high within-group variation (CV = 60%) rendered this difference non-significant. Fine-scale factors—slope position, gradient, and aspect—all significantly influenced biomass.

Slope position and gradient affect local soil thickness and consequently soil physicochemical properties, water, and nutrient conditions (Power et al., 1981; Woods & Schuman, 1988; Pachepsky et al., 2001; Chai et al., 2017). Generally, understory productivity is highest in valleys (with colluvial or alluvial soils). The higher biomass on steep slopes compared to gentle slopes, while unexpected, warrants discussion. First, steep slopes receive more lateral light from slope aspects than comparable gentle or flat slopes (the "steep slope effect"), enhancing productivity. Additionally, thin soils on steep slopes result in lower tree density and smaller stature (field observations), amplifying this effect. Mou and Warrillow (2000) noted similar patterns in ice storm impacts on sloped forests. Second, reduced litter accumulation on steep slopes may contribute to higher understory biomass (Xu et al., 2022). Higher biomass on flat terrain likely reflects superior soil conditions (Marques et al., 2004), while aspect differences may involve both light-temperature variations and moisture limitations (e.g., drier sunny slopes). In temperate humid regions, sunny slopes have better light and temperature but poorer moisture than shaded slopes; these interacting factors influence both tree and understory growth (Li, 2010). The significantly higher biomass on sunny slopes highlights light as a critical limiting factor, particularly given the extensive young secondary broadleaf forests with high density and canopy closure that create deep shade on flat and gentle slopes. In Changbai Mountains, Korean pine-broadleaf mixed forests allocate 89.9%, 3.4%, and 6.7% of total ecosystem photosynthesis to overstory, shrub, and herb layers, respectively (Wang et al., 2006), indicating light limitation for understory vegetation, which indirectly supports our findings.

Microtopographic effects on understory biomass are widespread (Gilliam & Roberts, 2003). The significant position × aspect interaction demonstrates topographic complexity. Valley flats showed no significant aspect differences because all aspects occur under dense canopy with similar light conditions. Additionally, these areas typically have deep soils and concave topography that maintains good moisture, supporting moisture-indicator species like *Impatiens noli-tangere* across all aspects (Hiratsuka & Inoue, 2013). On upper slopes, biomass varied consistently with aspect, with light appearing more important than moisture. The higher biomass on flat lower slopes compared to sloped lower slopes and other combinations remains unexplained and requires further investigation.

3.2 Ordinal Logistic Regression Analysis

Given the complex growth and distribution patterns of understory vegetation, using topography as an integrated predictor offers a viable approach for biomass probability estimation. Our logistic regression of 1,685 quadrats revealed: (1) Valley topographic combinations had high probabilities of high biomass; (2) Lower slope combinations had high probabilities of low biomass; (3) Sunny-steep slopes showed high probabilities of high biomass; (4) These patterns differed little between high and low elevations.

Some results were unexpected, such as relatively high high-biomass probabilities on environmentally harsh steep slopes (Zhao et al., 2012). At high elevations, both shaded- and sunny-steep slopes on upper positions had the highest high-biomass probabilities, while low-elevation lower slopes—typically favorable environments—showed high probabilities of low biomass. The "steep slope effect" with better light exposure provides a plausible explanation, supported by consistent aspect differences across elevations and positions. However, lower grazing intensity and human disturbance on steep slopes, particularly at high elevations, also contribute (Feng et al., 2021). Quantifying these specific effects requires controlled experiments.

Lower slopes with deep soils and good moisture-nutrient conditions should support high productivity and biomass (Liu et al., 2018), yet our observations and model predictions contradict this expectation. While favorable conditions should promote tree growth, field surveys showed lower mean tree diameter at breast height on lower slopes (Wang et al., 2019b). These areas are near villages and roads, easily accessible, and represent preferred forest grazing sites with high livestock (cattle) activity (Wang et al., 2019a) and greater human activity density than remote high-elevation areas. Probability estimates based on data including these disturbances have limitations for assessing productivity. Accurate productivity estimates require multi-year exclosure experiments, representing an important future research direction.

Conclusion

Topographic factors (slope position, aspect, and gradient) significantly influence closed forest understory biomass, which varies markedly across topographic combinations. Valley biomass exceeds upper slopes, which exceed lower slopes ($P < 0.01$). Shaded slope biomass is significantly lower than sunny slopes and flat terrain ($P < 0.01$), with no difference between the latter two. Among gradients, steep slopes > moderate slopes > gentle slopes ($P < 0.01$). The position × aspect interaction is significant, with flat lower slopes, flat upper slopes, sunny upper slopes, and all valley positions showing the highest biomass, while shaded lower slopes, sunny lower slopes, and shaded upper slopes show the lowest biomass. Under current conditions with human disturbance and forest grazing, valleys and steep slopes have the highest probability of high understory biomass production.

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