

Article

Regeneration Density and Morphometric Diversity of Qinghai Spruce Secondary Forests in the Qilian Mountains, Northwest China

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Abstract

Qinghai spruce (*Picea crassifolia* Kom.) secondary forests in the Qilian Mountains are pivotal for water conservation and biodiversity maintenance in arid northwest China. Based on a 10.2 ha permanent monitoring plot, we employed piecewise structural equation modeling (piecewise SEM) to analyze 47 indicators covering topography, stand structure, ground cover, and soil properties. Canopy openness (CO), moss–litter thickness (MLT), and herbaceous biomass (HB) exerted significant positive effects on the regeneration density (RD) in Qinghai spruce secondary forests, while crown width (CW) exerted a negative regulatory effect on this indicator. HB, altitude (AL), and leaf area index (LAI) exerted positive promoting effects on the regeneration morphometric diversity, whereas soil organic carbon (SOC) imposed strong inhibitory effects on this diversity metric. MLT, AL, SOC, and CW were identified as four shared regulatory factors that simultaneously shape regeneration density and seedling morphometric diversity in these alpine forest ecosystems, verifying the third research hypothesis. Maintaining CO at 0.5–0.6 and retaining 5–6 cm MLT can effectively facilitate natural regeneration. This study provides quantitative threshold references for ecological restoration and refined sustainable management of alpine coniferous spruce forests in arid mountainous regions.

Keywords: alpine coniferous forest; piecewise structural equation model; soil organic carbon; natural forest regeneration; alpine ecosystem restoration

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1. Introduction

Forests provide essential ecosystem services, including biodiversity conservation and water supply, which are critical for human survival and development [1]. Natural forests in the arid Qilian Mountains of northwest China act as a key ecological barrier

safeguarding downstream water security and biodiversity [2]. As the dominant constructive species of alpine ecosystems in this region, secondary forests of Qinghai spruce (*Picea crassifolia* Kom.) deliver vital functions such as water conservation, soil protection, and carbon sequestration, underpinning the stability of arid and semi-arid mountain ecosystems [3]. Natural regeneration determines forest succession, stand stability, and functional sustainability. Here, regeneration morphometric diversity refers to the morphological heterogeneity of seedlings reflected by ground diameter, height, and crown width. This metric directly mirrors seedling adaptability and stand development potential and, thus, strongly shapes stand development, adaptability, and ecosystem resilience [4,5]. Maintaining natural regeneration and healthy morphometric diversity can stabilize forest structure and sustain key ecological processes, including seed dispersal, seedling establishment, and tree growth, and sustain mountain ecosystem services such as water conservation for downstream stakeholders [6,7]. Quantitative evaluation of forest regeneration morphometric diversity and regeneration status requires multiple indicators such as diameter at breast height, tree height, crown dimension, stem form, basal area, and size-class heterogeneity [8]. Regeneration density and morphometric diversity of Qinghai spruce are co-regulated by above-ground stand structure, ground cover, and below-ground soil properties under alpine semi-humid climatic constraints. However, under climate warming, permafrost degradation, and anthropogenic disturbances (grazing, thinning, fuelwood harvesting), Qinghai spruce forests have suffered severe regeneration degradation featured by low seedling survival, stunted growth, uneven spatial distribution, and reduced morphometric diversity, which hinders forest restoration and weakens ecosystem services [2,9,10].

Studies across temperate montane coniferous ecosystems widely demonstrate that natural seedling recruitment is jointly regulated by topographic features, stand architecture, understory ground cover, and soil properties [11,12]. Empirical work on *Larix gmelinii* forests in the Greater Khingan Mountains exemplifies such interactive regulation: stand structural attributes exert stronger controls over seedling density than soil-related variables, whereas heterogeneity in regenerative diversity is predominantly shaped by soil biochemistry and site topography [12]. Recent research focused on Qinghai spruce has examined recruitment responses to elevational gradients and soil stoichiometric variation, yet few studies implement piecewise structural equation modeling (piecewise SEM) to untangle the intertwined multi-factor interactions that govern seedling colonization and survival [13–15].

Despite these foundational findings, critical limitations still constrain current understanding of Qinghai spruce regeneration mechanisms. Most published analyses adopt univariate statistical approaches and fail to quantify synergistic couplings between stand structure, ground cover, and soil properties, leaving the complete causal chains driving seedling recruitment unresolved [3,13]. Traditional structural equation modeling (SEM) presents inherent analytical limitations for forest inventory data; the method cannot readily account for spatial autocorrelation among sampling points, non-normal error distributions, and modest sample sizes, making it difficult to quantitatively disentangle direct versus indirect environmental effects on seedling performance [16]. Alpine arid spruce systems also lack targeted research on their endemic functional processes, such as microclimate buffering from moss–litter strata and the alkalinity-driven soil acidification mitigation effect, limiting holistic interpretation of recruitment strategies specialized to this harsh mountain setting.

Accordingly, this study proposes three interrelated scientific hypotheses. First and foremost, canopy structure and ground cover traits impose dominant direct controls on regeneration density, while topography and soil factors act mainly through indirect path-

ways. In addition, seedling morphometric diversity is more sensitive to topographic heterogeneity and soil organic carbon than to stand structural attributes. In this study, sensitivity refers to the degree of seedling morphological differentiation driven by environmental variation. Topography and soil organic carbon alter fine-scale resource availability to generate rapid trait differences among seedlings, while stand structure regulates understory light competition slowly and triggers milder morphological variation. Third, four core shared environmental factors, including moss–litter thickness, altitude, soil organic carbon, and crown width, simultaneously control regeneration density and seedling morphometric diversity through disparate ecological pathways: moss–litter thickness and altitude promote both regeneration indicators by optimizing understory hydrothermal microhabitats; soil organic carbon inhibits seedling morphological differentiation, whereas large crown width suppresses total seedling density via canopy light competition. Piecewise structural equation modeling (piecewise SEM) addresses the critical limitations inherent to conventional SEM frameworks mentioned above, which cannot untangle the intricate multi-layered causal relationships between environmental covariates and seedling regeneration metrics in alpine mountain forests. The conventional method’s statistical constraints elaborated earlier impede reliable differentiation of direct and indirect environmental effects on seedling recruitment. This analysis leverages hierarchical model decomposition and Shipley’s separation test to relax strict statistical assumptions, rendering it a robust analytical tool for the multi-factor ecological dataset collected in this study [17]. Using field data collected from a 10.2 ha permanent monitoring plot in the Qilian Mountains, we adopted piecewise structural equation modeling (piecewise SEM) to quantify the direct and indirect effects of 47 environmental predictors (Table 1) on two core seedling recruitment indicators: regeneration density and seedling morphometric diversity. In line with our three interconnected hypotheses proposed above, morphometric diversity quantifies the morphological heterogeneity of Qinghai spruce seedlings based on variations in seedling ground diameter, height, and crown width, a trait that directly reflects seedling adaptability and the long-term developmental potential of forest stands. We further identify shared core regulatory factors and their quantitative ecological thresholds that jointly modulate both regeneration metrics. This study will elucidate the multi-factor coupled mechanisms underlying natural seedling recruitment in temperate alpine secondary forests dominated by Qinghai spruce and will provide quantitative empirical references to support targeted ecological restoration and refined sustainable forest management across mountainous landscapes of the Qilian Mountains.

Table 1. Baseline descriptive statistics for all explanatory and response variables across sampling plots of Qinghai spruce forests, Qilian Mountains (n = 125).

Variable Group	Observed Variable	Value Range	Mean	SD	Skewness	Kurtosis
Topographic	AL (m)	2857.15–2944.10	2888.63	18.35	0.704	0.079
	SL (°)	3.36–35.82	15.99	6.19	0.513	−0.058
	AS (°)	1.33–358.24	151.99	137.45	0.56	−1.515
	CU	−4.42–3.64	−0.28	1.46	0.051	0.44
Spatial structure	U	0.00–1.00	0.40	0.24	−0.232	−0.333
	R	0.00–4.98	0.99	0.84	1.512	3.419
	B	0.00–1.60	0.47	0.31	1.073	1.575
	W	0.00–1.00	0.52	0.21	−0.815	1.862
	CI	0.00–44.07	8.53	9.43	1.408	1.809
	C	0.00–1.00	0.81	0.31	−1.800	1.868
Non-spatial structure	LAI	0.44–1.63	1.34	0.17	−1.914	7.421
	MLA (°)	3.41–89.75	51.96	15.03	−0.102	0.98
	VO (%)	27.21–71.78	34.54	6.06	3.203	14.097
	DBH (cm)	0.00–44.40	11.90	10.32	0.934	0.103
	H (m)	0.00–24.20	7.73	6.12	0.838	0.031

	CW (m)	0.00–7.35	2.56	1.67	0.473	−0.199
	TD (ind·ha ^{−1})	0.00–15,200.00	2192.00	2788.73	2.609	7.999
	V (m ³ ·ha ^{−1})	0.00–580.00	153.59	153.21	1.066	0.283
Ground cover layer	HC (%)	2.00–97.00	28.63	24.73	1.225	0.456
	HB (g·m ^{−2})	0.83–693.64	65.41	104.93	3.252	12.366
	MLT (cm)	0.00–18.60	5.65	3.02	1.515	3.913
	BLC (%)	0.00–100.00	78.62	18.23	−1.042	1.433
	BLB (kg·m ^{−2})	0.00–19.16	6.77	2.82	1.025	2.678
Soil	OC (g·kg ^{−1})	50.85–70.98	59.55	4.60	0.521	−0.487
	AP (mg·kg ^{−1})	4.18–47.20	16.05	8.80	0.916	0.243
	NN (mg·kg ^{−1})	0.01–0.62	0.16	0.10	1.627	3.561
	AN (mg·kg ^{−1})	0.85–3.22	1.85	0.63	0.335	−0.949
	pH	7.15–7.54	7.35	0.08	−0.071	−0.08
Mature trees diversity	H _H	0.00–3.01	1.10	0.88	0.123	−1.149
	D _H	0.00–0.94	0.53	0.36	−0.616	−1.337
	J _H	0.00–1.00	0.69	0.45	−0.898	−1.204
	H _{DBH}	0.00–3.29	1.11	0.91	0.265	−0.876
	D _{DBH}	0.00–0.96	0.52	0.36	−0.588	−1.349
	J _{DBH}	0.00–1.00	0.69	0.45	−0.893	−1.207
	H _{CW}	0.00–2.75	1.08	0.87	0.117	−1.22
	D _{CW}	0.00–0.93	0.52	0.36	−0.573	−1.377
	J _{CW}	0.00–1.00	0.69	0.45	−0.892	−1.208
Regeneration density and diversity	RD (ind·ha ^{−1})	400.00–61,600.00	13,212.80	14,293.24	1.595	2.002
	H _{RH}	0.00–4.28	2.39	0.95	−0.068	−0.572
	D _{RH}	0.00–0.98	0.85	0.16	−3.029	13.158
	J _{RH}	0.00–1.00	0.95	0.13	−6.644	47.688
	H _{RGD}	0.00–4.99	2.86	1.17	−0.204	−0.819
	D _{RGD}	0.00–0.99	0.89	0.15	−3.447	16.37
	J _{RGD}	0.00–1.00	0.98	0.13	−7.789	59.728
	H _{RCW}	0.00–4.42	2.50	0.95	−0.2	−0.513
	D _{RCW}	0.00–0.99	0.87	0.15	−3.448	16.733
	J _{RCW}	0.00–1.00	0.96	0.13	−7.115	52.639

(Note: AL: Altitude, SL: Slope, AS: Aspect, CU: Curvature, U: Size ratio (neighborhood comparison), R: Aggregation Index (Almax), B: Canopy Openness, W: Uniform angle index, CI: Competition index, C: Density, LAI: Leaf area index, MLA: Mean leaf angle, VO: Porosity/Canopy gap fraction, DBH: Diameter at breast height, H: Tree height, CW: Crown width, TD: Tree density, V: Stand Volume, HC: Herbaceous cover, HB: Herbaceous biomass, MLT: Moss–litter thickness, BLC: Bryophyte and litter coverage, BLB: Bryophyte and litter biomass, OC: Organic carbon, AP: Readily available phosphorus, NN: Nitrate nitrogen, AN: Ammonium nitrogen, H: Shannon Diversity Index, D: Simpson Diversity Index, J: Pielou Evenness Index, RD: Regeneration density, RH: Regeneration height, RGD: Regeneration ground diameter, RCW: Regeneration crown width.)

2. Materials and Methods

2.1. Introduction to Study Area

The Dayekou watershed is in the center of the northern slopes of the Qilian Mountains. The watershed covers an area of 68.06 km², with an elevation range from 2650 to 4600 m. The average annual precipitation is 400 mm, evaporation is 1488 mm, relative humidity is 60%, and air temperature is 5.4 °C. The mean air temperature of the warmest month is 19.6 °C, and of the coldest month is −12.5 °C. The region has a temperate continental high-cold, semi-humid mountain climate [18]. In this area, the precipitation and temperature are synchronized throughout the year, while winters are cold and damp [14]. Under these harsh climatic conditions, the distribution of vegetation exhibits significant altitudinal gradients, which are also reflected in the soil types associated with the different vegetation zones. From lower to higher elevations, the vegetation and soil types are distributed as follows: typical mountain shrub-grassland belt (chestnut soil), cold-temperate

coniferous forest belt (gray–brown soil), alpine shrub–meadow belt (shrub–meadow soil), and alpine sub-ice and snow sparse vegetation belt (cold desert soil).

On shaded and semi-shaded slopes, that is, north-facing slopes, Qinghai spruce and various shrub species are interspersed with grasslands. Scattered Qilian juniper (*Juniperus przewalskii* Kom.) forests are found on sunny slopes, forming a distinct forest–grassland mosaic landscape within the watershed. Due to limited water and heat availability, plant species diversity is relatively low [19]. Apart from Qinghai spruce, which dominates the Dayekou watershed, shrub species such as *Salix gilashanica* C.Wang et P.Y.Fu, *Potentilla fruticosa* L., *Potentilla glabra* Lodd., *Caragana jubata* (Pall.) Poir., and *Spiraea alpina* Pall. are also present. Dominant herbaceous species include *Carex atrata* L., *Potentilla chinensis* Ser., *Polygonum viviparum* L., *Iris lactea* Pall., and *Stellera chamaejasme* L., respectively. Mosses, such as *Plagiomnium cuspidatum* (Hedw.) T.J.Kop., *Abietinella abietina* (Hedw.) M.Fleisch., and *Hypnum cupressiforme* Hedw. are commonly found on forest floors.

2.2. Plot Design and Field Survey

The permanent monitoring plot for Qinghai spruce measures 300 m × 340 m (102,000 m², corresponding to 10.2 ha) and was established between 2010 and 2011 by the National Qilian Mountains Forest Ecosystem Research Station (Figures 1 and 2). The terrain is relatively flat, and the arbor layer in the plot is purely composed of Qinghai spruce. The entire sample plot was strictly established in accordance with the survey technical specifications of the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute (STRI), USA [20,21]; the detailed information on the plot can be found in [18].

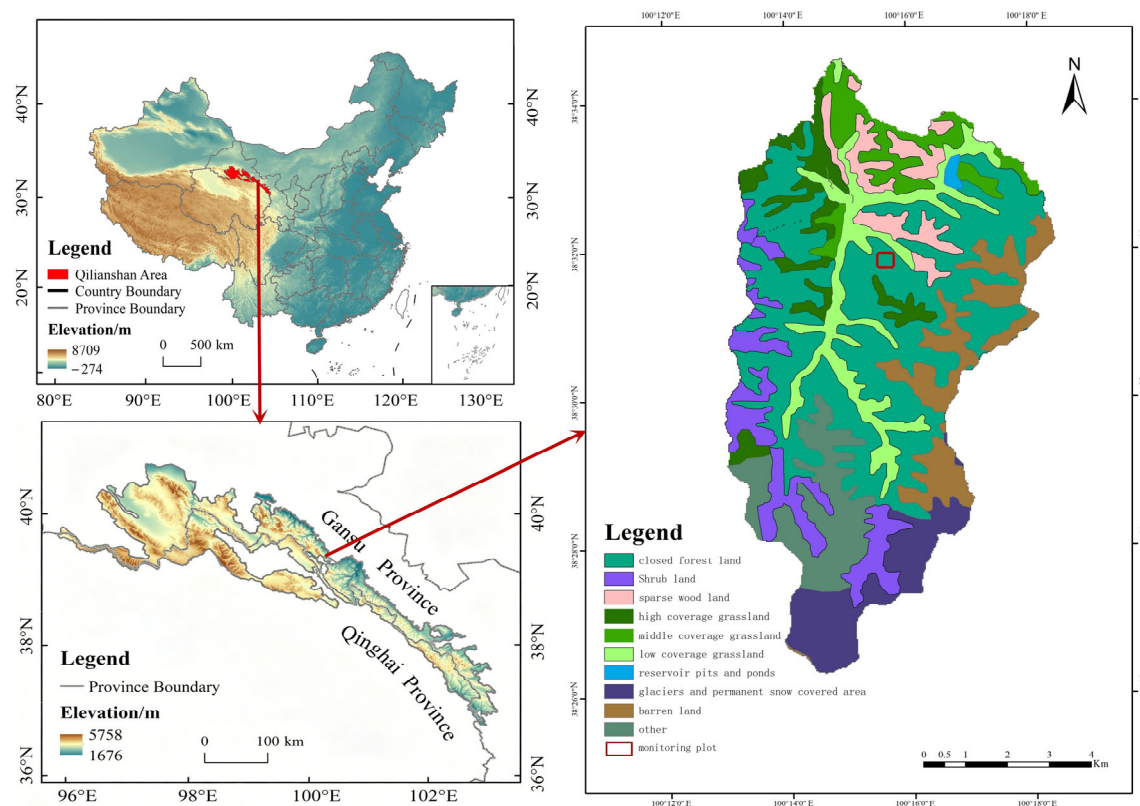


Figure 1. Geographic location and land cover map of the 10.2 ha permanent dynamic monitoring plot for Qinghai spruce secondary forest, located within the Dayekou watershed on the northern slope of the Qilian Mountains, Gansu Province, northwest China. The map displays land cover types that are clearly classified into closed forest land, shrub land, sparse woodland, high/medium/low

coverage grassland, glaciers and permanent snow cover, reservoirs, and barren land, reflecting the typical mountain landscape pattern of forest–shrub–grassland mosaics in this arid alpine region. The Dayekou watershed covers a total area of 68.06 km² with a regional elevation span of 2650–4600 m, where the 10.2 ha monitoring plot is centrally situated at a middle-to-high altitude zone with prominent local topographic and altitudinal variation.

This study applied the space-for-time substitution approach and referred to widely accepted alpine forest regeneration classification standards suitable for Qinghai spruce growth characteristics to classify all living individuals with a height less than 1.5 m and a ground diameter less than 5.0 cm as regeneration seedlings. Individuals with a height of ≥ 1.5 m and DBH ≥ 5.0 cm were classified as mature trees [22–24].

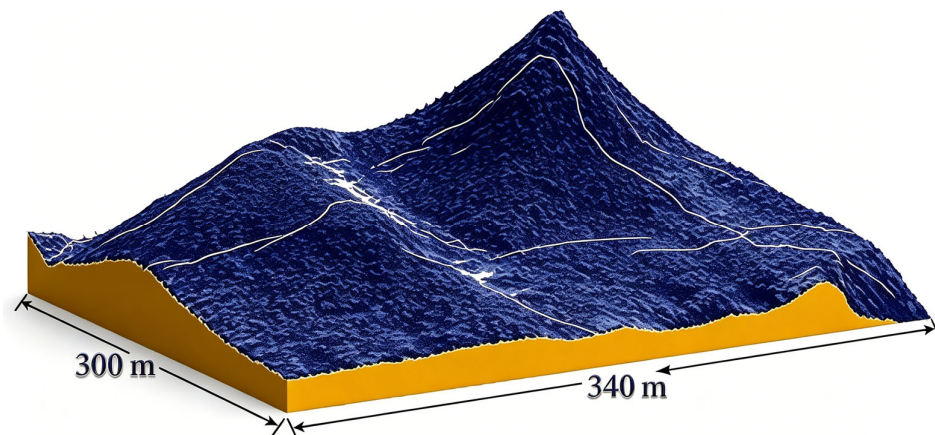


Figure 2. The 3D topographic map of the 300 m × 340 m dynamic monitoring plot for Qinghai spruce forest in the Dayekou watershed, Qilian Mountains.

Based on geostatistical principles [25], the plot was divided into 255 subplots of 20 m × 20 m via total station theodolite precise 3D positioning. Each subplot was further divided into sixteen 5 m × 5 m grid cells, forming 4080 grid cells in total. To balance environmental gradient representativeness, community heterogeneity, and field operability, the bottom-left 5 m × 5 m grid of each subplot was selected as the basic survey unit, forming 255 microplots. Field surveys confirmed that 130 microplots had no Qinghai spruce regeneration seedlings, and only 125 microplots had effective regeneration seedlings; these 125 microplots with target seedlings were used for subsequent statistical analysis and modeling. Field investigations were conducted from July to September 2024. For each individual seedling and mature tree, relative coordinates (x, y), height, crown width, ground diameter (seedlings), DBH (mature trees), and growth status (alive, dead, fallen) were measured and recorded.

2.3. Forest Regeneration

This study adopts classical analytical methods for tree regeneration and its driving factors in temperate and alpine forests [26–28] and establishes a targeted framework tailored to the growth traits of Qinghai spruce in the Qilian Mountains. A multi-dimensional variable system was constructed to quantify drivers of seedling regeneration density and morphometric diversity, encompassing a full suite of above-ground predictors and below-ground soil physicochemical attributes; all measured variables and their classifications are comprehensively listed in Table 1. Regeneration density (RD) and the Shannon diversity index of seedling ground diameter (HRGD, the representative metric for seedling morphometric diversity quantifying morphological divergence among juvenile Qinghai

spruce seedlings) were defined as response variables, with six-dimensional environmental and structural indicators as predictors. Measured plant and soil variables were classified as hard functional traits (fixed intrinsic organismal attributes: DBH, tree height, crown width, and soil organic carbon) and soft functional traits (plastic community-level attributes: diversity indices, herbaceous biomass, and canopy openness), following the classification scheme of Bell et al. [29]. Topographic metrics (altitude, slope) were excluded from this trait grouping and treated as external environmental covariates, given they reflect site-level conditions rather than inherent or plastic biological characteristics of individual trees or seedling assemblages. This classification scheme disentangles how biological traits respond differently to surrounding environmental gradients.

Topographic factors (altitude, slope, aspect, curvature) were derived from total station-surveyed 3D terrain data. Spatial stand structure indicators included angle scale, size ratio, canopy openness, aggregation index, competition index, and stand density [30]; canopy openness was measured via hemispherical canopy photography, and other parameters were calculated in Winkelmass 1.8 software with a fixed 5 m buffer radius. Non-spatial stand structure indicators (leaf area index, mean leaf angle, canopy gap fraction, mean DBH, mean tree height, mean crown width, stem density, and stand volume) were measured using a plant canopy analyzer, field surveys, and the local volume formula for Qinghai spruce. Ground cover indicators (herbaceous cover, herbaceous biomass, moss–litter thickness, moss–litter cover, and moss–litter biomass) were obtained via visual estimation, destructive sampling (oven-dried at 85 °C to constant weight), and field measurement. Soil indicators (organic carbon, available phosphorus, nitrate nitrogen, ammonium nitrogen, and pH) were analyzed using standard laboratory methods for 0–10 cm surface soil samples.

Mature tree morphometric diversity was quantified using Shannon, Simpson, and Pielou indices based on tree height, DBH, and crown width [31,32]. Regeneration indicators targeted seedlings (height < 1.5 m, ground diameter < 5.0 cm) [15], including regeneration density and morphometric diversity (Shannon, Simpson, and Pielou indices for height, ground diameter, and crown width), with HRGD as the representative diversity index. As the plot is a pure Qinghai spruce secondary forest, all variables were treated as continuous. The analytical workflow included descriptive statistics, Pearson correlation, VIF multicollinearity diagnosis, Global Moran's I spatial autocorrelation test, diversity index calculation, and piecewise SEM; all formulas are presented in Table 2, with standardization ensured per classical forest ecological methods.

Table 2. Calculation formulae for stand spatial structure and diversity indices.

Index	Calculation Formula	Note
W	$W_i = \frac{1}{n} \sum_{j=1}^n z_{ij}$	W_i is the angular scale of the i -th central tree. If the i -th α angle is less than the standard angle α_0 , then $z_{ij} = 1$, otherwise $z_{ij} = 0$
U	$U_i = \frac{1}{n} \sum_{j=1}^n k_{ij}$	U_i is the i -th size ratio value of the tree species. If the adjacent tree j is smaller than the reference tree i in terms of DBH, then $k_{ij} = 1$, otherwise $k_{ij} = 0$
H	$H = - \sum_{i=1}^n \frac{B_i}{N} \left(\ln \frac{B_i}{N} \right)$	N is the total number of individuals in the microplot, B_i is the number of individuals of the i -th species in the microplot
D	$D = 1 - \sum_{i=1}^n p_i^2$	p_i is the ratio of the number of individuals of the i -th tree species to the total number of individuals in the sample plot
J	$J = H/\ln S$	S is the total number of species in the sample plot

(Note: W: Angle scale; U: Size ratio; H: Species-based Shannon diversity index; D: Species-based Simpson diversity index; J: Species-based Pielou evenness index. For this study's core morphometric diversity analysis, the identical Shannon formula was applied to seedling ground diameter data to

calculate HRGD, which quantifies morphological divergence among juvenile Qinghai spruce seedlings as defined in the Introduction. The ground-diameter-derived Pielou evenness index correspondingly reflects the uniformity of seedling size distribution, providing dedicated interpretive context for morphological trait variation across microhabitats).

2.4. Statistical Analysis

All variables were standardized via Z-score transformation ($Z = (X - \mu)/\sigma$) prior to correlation analysis, multicollinearity diagnosis, and piecewise SEM construction to eliminate dimensional discrepancies. A two-step variable screening strategy was implemented: key variables were preliminarily selected via two-tailed Pearson correlation analysis ($p < 0.10$), and highly collinear variables were removed using the Variance Inflation Factor (VIF) combined with Generalized Linear Model (GLM), with only variables of VIF < 5 retained for model building.

Global Moran's I index was calculated in R 3.6.2 using the stats and sped packages to test spatial autocorrelation of regeneration density (RD) and regeneration morphometric diversity (HRGD) [33]; no significant spatial autocorrelation was detected ($p > 0.05$), satisfying the independent observation assumption for piecewise SEM. All retained predictors were assigned to fixed or random groups for hierarchical piecewise SEM construction, following the analytical framework of Lefcheck [17]. Only canopy openness was treated as a fixed variable, as silvicultural thinning can directly regulate this stand attribute. Altitude and slope (topographic factors), moss–litter thickness and herbaceous biomass (ground cover metrics), soil organic carbon and tree density were classified as random microhabitat covariates. Moss–litter thickness and soil organic carbon are driven by fine-scale, unmanaged spatial heterogeneity of microclimate and soil substrates, rather than artificial forest management, justifying their reallocation to the random group.

Piecewise SEM was constructed using the piecewise SEM package in R 3.6.2, following the theoretical framework of piecewise SEM [34], with model goodness-of-fit evaluated by χ^2 test and Fisher's C test ($p > 0.05$ indicates acceptable fit). Path effects were decomposed into direct, indirect, and total effects. Stand spatial structure parameters (uniform angle index, size ratio) were calculated in Winkelmass 1.8 software with a fixed 5 m buffer radius [35], and all other indicator calculations and data collation were completed in Excel 2019 to ensure result standardization and repeatability.

3. Results

3.1. Basic Characteristics of Observed Variables

The average elevation of the experimental plot is 2888.63 m, with an absolute altitudinal range from 2857.15 m to 2944.10 m, yielding a total local elevation variation of 86.95 m. This substantial absolute altitudinal fluctuation forms a distinct middle-to-high elevation micro-gradient within the broader Dayekou watershed elevation scope of 2650–4600 m (Table 1). The slope gradient varied between 3.36° and 35.82° , with an average of 15.99° . For soil attributes, soil organic carbon content ranged from $50.85 \text{ g}\cdot\text{kg}^{-1}$ to $70.98 \text{ g}\cdot\text{kg}^{-1}$, averaging $59.55 \text{ g}\cdot\text{kg}^{-1}$, while the mean soil pH was 7.35, showing weak alkalinity. Stand tree density varied widely from 0.00 to $15,200.00 \text{ ind}\cdot\text{ha}^{-1}$, with a mean of $2192.00 \text{ ind}\cdot\text{ha}^{-1}$; the mean crown width was 2.56 m, and the mean stand volume reached $153.59 \text{ m}^3\cdot\text{ha}^{-1}$. The moss–litter thickness ranged from 0.00 to 18.60 cm with a mean of 5.65 cm, and herbaceous biomass ranged from 0.83 to $693.64 \text{ g}\cdot\text{m}^{-2}$ with an average of $65.41 \text{ g}\cdot\text{m}^{-2}$. The mean uniform angle index was 0.52, and the mean size ratio was 0.40, reflecting the numerical distribution of stand spatial structure indicators across the plot.

3.2. Correlation Analysis of Observed Variables

Among all observed pairs, most pairs of factors showed significant correlations to varying degrees (Figure 3). Among them, the regeneration density was significantly and positively correlated with the thickness of moss–litter ($r = 0.238$, $p = 0.007$), herbaceous biomass ($r = 0.205$, $p = 0.022$), and canopy openness ($r = 0.209$, $p = 0.020$). In addition, it was significantly negatively correlated with crown width ($r = -0.177$, $p = 0.048$), and regeneration diversity (represented by the Shannon index of regeneration crown width). Finally, it was significantly and positively correlated with altitude ($r = 0.378$, $p < 0.001$), slope ($r = 0.349$, $p < 0.001$), and herbaceous biomass ($r = 0.191$, $p = 0.033$), and was significantly negatively correlated with organic carbon ($r = -0.373$, $p < 0.001$) and crown width ($r = -0.204$, $p = 0.022$).

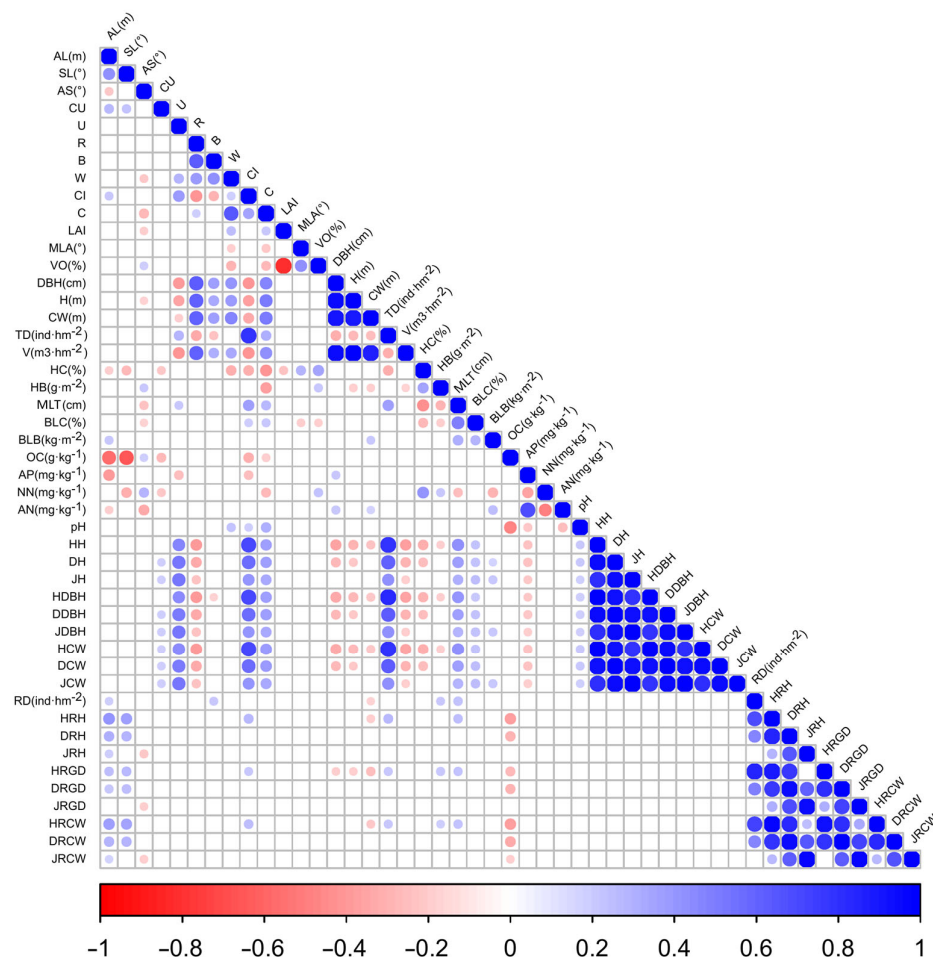


Figure 3. Correlation analysis of measured variables and calculated indices of Qinghai spruce forests in the Qilian Mountains ($p < 0.05$).

For topographic factors, altitude was significantly and positively correlated with slope ($r = 0.213$, $p = 0.014$). For the soil factors, organic carbon was significantly and positively correlated with available phosphorus ($r = 0.286$, $p = 0.001$). For the stand structure factors, plant density was significantly and negatively correlated with crown width ($r = -0.242$, $p = 0.006$), and significantly positively correlated with volume ($r = 0.635$, $p < 0.001$). For the ground cover layer, moss–litter thickness was significantly negatively correlated with herbaceous biomass ($r = -0.281$, $p = 0.001$).

3.3. Factors Influencing Regeneration Density Diversity of Qinghai Spruce Forest

3.3.1. Variable Selection

Based on preset screening criteria (correlation with regeneration density and statistical significance) and verified through correlation analysis, eight indicators, including moss–litter thickness (MLT), canopy openness (B), herbaceous biomass (HB), altitude (AL), crown width (CW), slope (SL), organic carbon (OC), and tree density (TD), were ultimately selected as the observed variables in the piecewise SEM for regeneration density. The correlations between these variables and regeneration density showed that SL, OC, and TD were significant at the $p < 0.10$ level, while the remaining indicators reached the significance level of $p < 0.05$ (Table 3).

Table 3. The Correlation coefficients and significance among the regeneration density and the final eight selected indicators.

Variables	r	p
MLT (cm)	0.238	0.007
B	0.209	0.020
HB (g·m ⁻²)	0.205	0.022
AL (m)	0.184	0.040
CW (m)	−0.177	0.048
SL (°)	0.175	0.051
OC (g·kg ⁻¹)	−0.162	0.071
TD (ind·ha ⁻¹)	0.150	0.094

3.3.2. Piecewise SEM Construction for Regeneration Density

The selected regeneration variables and regeneration density were used to construct and test the piecewise SEM. The global fit indices of the model showed that: $\chi^2 = 10.601$, $p = 0.717$ (degrees of freedom = 14), $p > 0.05$; Fisher's C = 23.025, $p = 0.732$ (degrees of freedom = 28), indicating that the model fit was good. All p -values for the independent assumptions are greater than 0.05, indicating that the model's setting did not significantly violate the independence assumption.

The piecewise SEM reveals that the model can explain 26% of the variation in seedling regeneration density of Qinghai spruce forests ($R^2 = 0.26$). All core controllable factors for forest management (canopy openness, moss–litter thickness, herbaceous biomass, crown width, etc.) were included, and no key regulatory variables were omitted. The model still effectively quantifies the core driving effects of the selected observed variables on regeneration density (Figure 4). As shown in OC, it was significantly negatively affected by AL ($\beta = -0.37$, $p < 0.05$) and SL ($\beta = -0.49$, $p < 0.05$). HB was significantly negatively affected by MLT ($\beta = -0.281$, $p < 0.05$), indicating that an increase in MLT would inhibit the accumulation of HB. CW was significantly positively affected by B ($\beta = 0.402$, $p < 0.05$) and significantly negatively affected by HB ($\beta = -0.242$, $p < 0.05$). TD was significantly positively affected by MLT ($\beta = 0.365$, $p < 0.05$) and significantly negatively affected by CW ($\beta = -0.242$, $p < 0.05$). The significant paths of the final variable RD included the direct effects of MLT ($\beta = 0.256$), HB ($\beta = 0.228$), B ($\beta = 0.272$), and CW ($\beta = -0.224$), indicating that an increase in MLT, HB, and B would enhance RD, while an increase in CW would inhibit RD. A significant negative covariance was observed between TD and B ($\beta = -0.161$, $p = 0.037$). The path coefficient of the marginally significant path, TD~OC, was -0.1541 ($p = 0.058$) (Figure 5). The total effect of B was lower than the direct effect, and there was an inhibitory indirect effect in its path (such as through the negative influence of other variables).

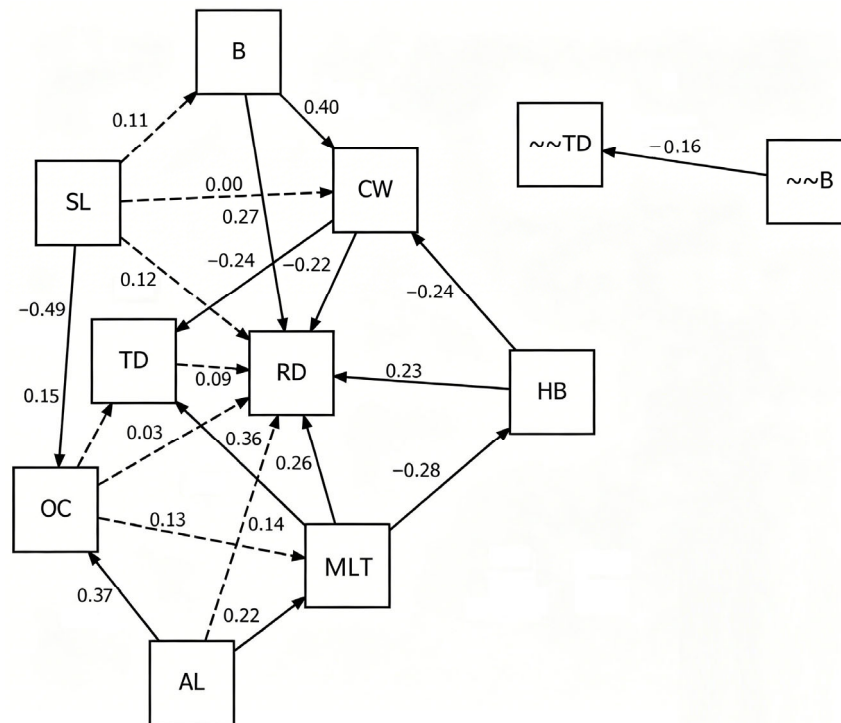


Figure 4. A diagram of the key pathway of the regeneration density piecewise SEM of Qinghai spruce forests in the Qilian Mountains. Note: AL: Altitude, SL: Slope, B: Canopy Openness, CW: Crown width; TD: Tree density, HB: Herbaceous biomass, MLT: Moss–litter thickness, OC: Organic carbon, RD: Regeneration density.

3.4. Factors Influencing Regeneration Morphometric Diversity of Qinghai Spruce Forest

3.4.1. Variable Selection

Ten indicators with relatively high correlation with the ground diameter Shannon diversity index (HRGD) were selected for the construction of the piecewise SEM. The screening results show that the leaf area index (LAI) and porosity/canopy gap fraction (VO, %) are significant at the $p < 0.10$ level, while the remaining eight indicators all reach the significant level of $p < 0.05$, meeting the statistical requirements for model construction (Table 4).

Table 4. The Pearson correlation coefficients (r) and level of significance (p) among the regeneration diversity and the final ten indicators selected.

Variables	r	p
AL (m)	0.378	<0.001
OC (g·kg ⁻¹)	−0.373	<0.001
SL (°)	0.349	<0.001
CI	0.249	0.005
MLT (cm)	0.232	0.009
TD (ind·ha ⁻¹)	0.215	0.016
CW (m)	−0.204	0.022
HB (g·m ⁻²)	0.191	0.033
LAI	0.171	0.056
VO (%)	−0.168	0.061

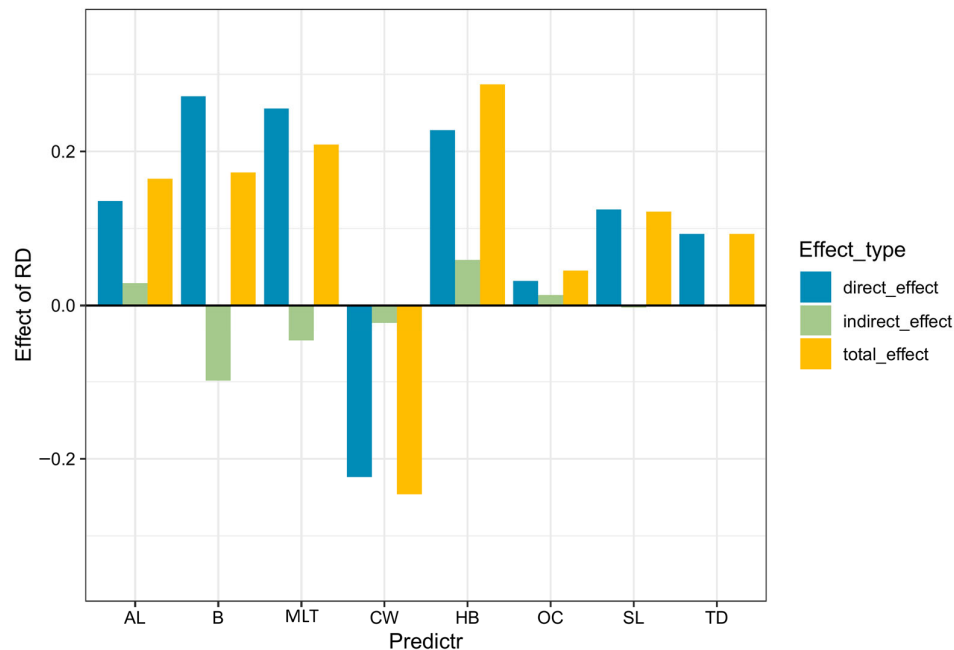


Figure 5. The impact of each measured variable on regeneration density of Qinghai spruce forests in the Qilian mountains. Note: AL: Altitude, B: Canopy Openness, MLT: Moss–litter thickness, CW: Crown width; HB: Herbaceous biomass, OC: Organic carbon, SL: Slope, TD: Tree density.

3.4.2. Piecewise SEM Construction for Regeneration Morphometric Diversity

The selected measured variables and regeneration morphometric diversity were used to construct and test the piecewise SEM. The global fit index of the model showed: $\chi^2 = 24.36$, $p = 0.711$ ($df = 29$), $p > 0.05$; Fisher's $C = 52.92$, $p = 0.664$ ($df = 58$), indicating that the model fits well. All p -values for the independent assumptions are greater than 0.05, indicating that the model's setting did not significantly violate the independence assumption (Figure 6).

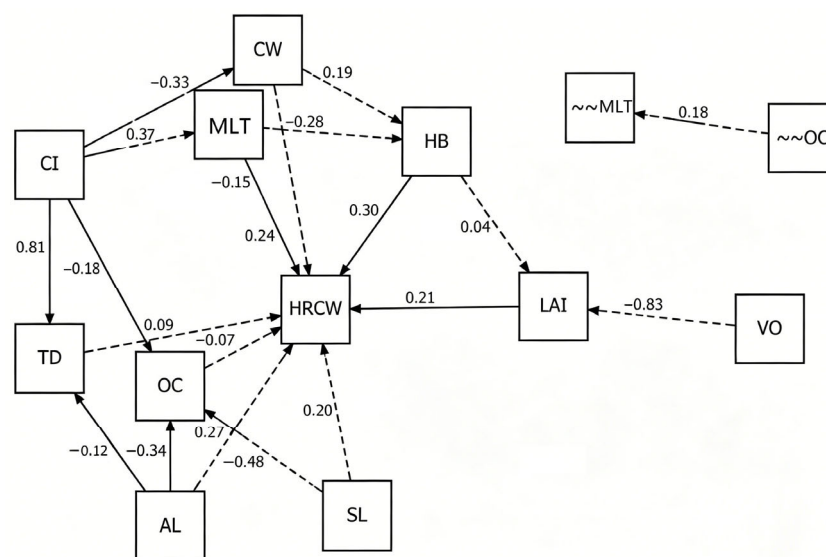


Figure 6. A diagram on the key pathway of piecewise SEM for regeneration of morphometric diversity of Qinghai spruce forests in the Qilian Mountains. Note: CI: Competition index, TD: Tree density, OC: Organic carbon, AL: Altitude, MLT: Moss–litter thickness, CW: Crown width, SL: Slope,

HB: Herbaceous biomass, LAI: Leaf area index, VO: Porosity/Canopy gap fraction, H: Tree height, R: Aggregation Index (Almax).

Piecewise SEM (Figure 6) revealed that the Shannon index of morphometric diversity of the seedlings of Qinghai spruce (H_{RCW}) accounted for 40% of the total variation. The organic carbon (OC) is mainly driven by topographic factors, such as altitude (AL, $\beta = -0.34$, $p < 0.001$) and slope (SL, $\beta = -0.48$, $p < 0.001$), both of which showed significant negative effects (Figures 6 and 7). The competition index (CI) indirectly affected the system by inhibiting the accumulation of organic carbon ($\beta = -0.18$, $p = 0.004$). The thickness of the moss–litter (MLT) was directly and positively affected by the competition index (CI) ($\beta = 0.37$, $p < 0.001$) and had a significant covariance relationship with OC ($r = 0.18$, $p = 0.019$), suggesting that the two may share unknown ecological processes. The herbaceous biomass (HB) was jointly inhibited by MLT ($\beta = -0.28$, $p = 0.001$) and crown width (CW) ($\beta = -0.19$, $p = 0.026$), reflecting the resource competition effect of the moss–litter thickness on the herbaceous layer. The leaf area index (LAI) was mainly regulated by herbaceous biomass ($\beta = 0.04$, $p = 0.445$) and canopy gap fraction (VO) ($\beta = -0.83$, $p < 0.001$), and the negative effect of the latter may be due to the threshold effect of vegetation density on light interception.

About 40% of the variation in HRCW was explained by the piecewise SEM ($R^2 = 0.40$), and its directly affecting driving factors were included. Positive effects are related to herbaceous biomass ($\beta = 0.30$, $p < 0.001$), leaf area index ($\beta = 0.21$, $p = 0.004$), altitude ($\beta = 0.27$, $p = 0.004$), and slope ($\beta = 0.20$, $p = 0.035$), while negative effects are related to crown width ($\beta = -0.15$, $p = 0.054$) and may inhibit lower ecological processes through canopy shading. Indirect pathways, such as competition index (CI), may promote moss–litter thickness (MLT) development and change plant density (TD), producing a positive indirect effect ($\beta = 0.21$), while canopy gap fraction (VO) has a significant negative indirect effect ($\beta = -0.18$) by reducing LAI.

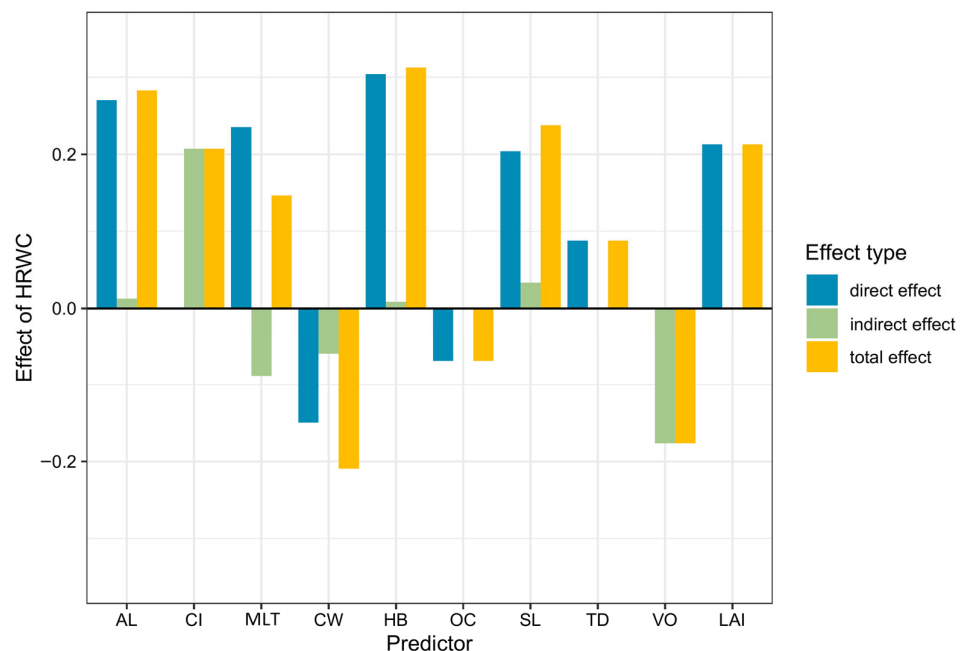


Figure 7. Impact of each selected factor on regeneration morphometric diversity of Qinghai spruce forests in the Qilian Mountains. Note: AL: Altitude, CI: Competition index, MLT: Moss–litter thickness, CW: Crown width, HB: Herbaceous biomass, OC: Organic carbon, SL: Slope, TD: Tree density, VO: Porosity/Canopy gap fraction, LAI: Leaf area index.

For the regeneration density structural equation model, the overall fitness performance was good, with a chi-square value of 10.601 ($df = 14$, $p > 0.05$) and Fisher's C value of 23.025 ($df = 28$, $p > 0.05$), and the model could explain 26% of the variation in regeneration density. The core direct influencing paths included canopy openness, moss–litter thickness, herbaceous biomass, and crown width. For the regeneration morphometric diversity model, the chi-square value was 24.36 ($df = 29$, $p > 0.05$), and Fisher's C value was 52.92 ($df = 58$, $p > 0.05$), with 40% of the variation in seedling morphometric diversity being explained (Table 5). Key direct driving factors included herbaceous biomass, altitude, leaf area index, and soil organic carbon. All fit indices of the piecewise SEM satisfied acceptable statistical thresholds, and path coefficients and corresponding significance levels for individual predictors are presented in the preceding results.

Table 5. Fitting indices, explanatory power, and standardized direct path coefficients of piecewise SEM for regeneration density and regeneration morphometric diversity of Qinghai spruce.

Parameter Category	Index	Regeneration Density	Morphometric Diversity
		Model	Model
Model fitting indices	χ^2	10.601	24.360
	Degrees of freedom (df)	14	29
	χ^2 p -value	0.717	0.711
	Fisher's C	23.025	52.920
	Fisher's C p -value	0.732	0.664
Explanatory power	Coefficient of determination (R^2)	0.26	0.40
Positive direct effect (β)	Canopy openness	0.272 *	—
	Moss–litter thickness	0.256 *	—
	Herbaceous biomass	0.228 *	0.300 *
	Altitude	—	0.270 *
	Leaf area index	—	0.210 *
	Slope	—	0.200 *
Negative direct effect (β)	Crown width	−0.224 *	−0.150 #
	Soil organic carbon	—	−0.340 *

Note: * $p < 0.05$; # Marginally significant ($0.05 < p < 0.06$); — indicates no significant path effect. All path coefficients are standardized for β values. The piecewise SEM achieves acceptable goodness-of-fit when both χ^2 and Fisher's C tests show insignificant p -values ($p > 0.05$).

4. Discussion

4.1. Ecological Significance and Regional Specificity of the Measured Variables

The measured variables of the Qinghai spruce secondary forest in the Qilian Mountains exhibit distinct regional characteristics. The average thickness of the moss–litter layer in the forest was 5.65 cm, which was significantly higher than that of the litter thickness of natural *Larix gmelinii* forests in the Lesser Khingan Mountains, where the average thickness was approximately 2.0 cm [36]. This pattern is driven by the cold, humid, high-altitude climate across the Qilian Mountains, which suppresses litter decomposition rates.

The mean soil organic carbon concentration ($59.55 \text{ g}\cdot\text{kg}^{-1}$) in the Qilian Mountains far exceeded the national average value for forest soils across China (approximately $24.56 \text{ g}\cdot\text{kg}^{-1}$) [37], demonstrating long-term carbon sequestration potential and strong ecosystem function and service capacity of Qinghai spruce forests. However, the slightly alkaline nature of these soils forms a sharp contrast with the acidic soils of Xing'an larch forests [38], a typical cold-temperate coniferous forest type in northern China. Most coniferous forest soils are naturally acidic, mainly driven by the decomposition of needle litter containing abundant tannins and organic acids, a widely acknowledged ecological pattern in temperate coniferous ecosystems. In contrast, the average soil pH of 7.35 measured in our

study area reflects weakly alkaline conditions. This pattern does not violate the general acidification trend of coniferous forest soils but arises from the unique pedogenic environment in the arid and semi-arid Qilian Mountains. The study area has well-developed calcic horizons enriched with calcium carbonate, which constitute a stable soil buffering system capable of neutralizing organic acids released during needle litter decomposition and sustaining soil pH within a weakly alkaline range. Furthermore, the cold, dry alpine climate slows litter decomposition rates and restricts the buildup of acidic metabolites, further inhibiting soil acidification. Soil acidification within Xing'an larch forests is primarily induced by intensive decomposition of tannin-rich needle litter and the consequent accumulation of organic acids [39], a ubiquitous feature of northern temperate coniferous forest soils. By comparison, the weak alkalinity of Qinghai spruce forest soils in the Qilian Mountains is tightly linked to the regional development of calcic horizons [40]. Calcium carbonate accumulated in such layers builds a robust buffering system that counteracts organic acids from litter decomposition, thereby maintaining soil pH at a weakly alkaline level [41].

The mean tree density was 2192.00 ind·ha⁻¹ with a coefficient of variation of 127%, indicating significant spatial heterogeneity in the stand density. This aligns with the findings of Tuo et al. [16] in the Dayekou watershed of the Qilian Mountains, where the Qinghai spruce population exhibits a mixed aggregated-random spatial distribution influenced by microtopography and disturbance history. The vertical distribution of Qinghai spruce was concentrated between elevations of 2857 and 2944 m, which is within the core mid-elevation range of Qinghai spruce distribution. The temperature and moisture regimes in the region optimally support the elevational distribution of Qinghai spruce. This corroborates the findings of Wang and Zhao [3] of a mid-elevation regeneration peak phenomenon. These features highlight unique roles of Qinghai spruce forests in regulating ecosystem services, including nutrient cycling and population distribution, and lay the groundwork for subsequent analyses of the influencing factors. This correlation pattern implies that increasing altitude and slope may suppress the accumulation of soil organic carbon.

4.2. Ecological Linkages Revealed by Variable Correlations

A significant negative correlation between moss–litter thickness and herbaceous biomass ($r = -0.281$, $p = 0.001$) was consistent with the litter-herb competition suppression hypothesis [42]. Specifically, a thick moss–litter thickness inhibits herb growth through physical barriers such as dense interwoven mats that impede seedling emergence and resource competition [42]. At the same time, herbaceous biomass in the Qilian mountains was positively correlated with the regeneration density of Qinghai spruce forest ($r = 0.205$, $p = 0.022$), which supports the findings of Ren et al. They found that moderate herbaceous cover promotes regeneration, possibly by reducing soil erosion at low cover levels while competition intensifies at high cover levels. This may also facilitate regeneration by creating a shading overlayer.

Elevation was negatively correlated with organic carbon ($r = -0.371$, $p < 0.001$) in the Qilian mountains. High-elevation larch forests in China's Guandi Mountains showed limited microbial activity at low temperatures, resulting in reduced carbon decomposition [43]. However, a positive correlation between elevation and regeneration diversity ($r = 0.378$, $p < 0.001$) in our study was different from that of the Korean pine regeneration study, which initially showed an increased trend followed by a decrease, along with the elevation [44]. This may be because at 2800–3000 m elevation of the Qilian Mountains, in which no Qinghai spruce has reached the upper limit distribution, and the temperature and humidity gradients of the increasing elevation of the mountain may remain within

the suitable range. The significant correlations between factor pairs indicate that the regeneration process of the Qinghai spruce forest is affected by the synergistic effects of multiple factors, and there is a complexity in the relationships among variables. Piecewise SEM successfully quantified and extracted the key controllable factors affecting regeneration density and diversity. The correlations suggest that the coupling effects of topography, soil, and ground cover are fundamental to the regeneration process of Qinghai spruce forests in the Qilian mountains.

4.3. Driving Mechanisms of Regeneration Density and the Regulatory Role of Stand Structure

Piecewise SEM showed that canopy openness (B) has the greatest and direct effects on regeneration density ($\beta = 0.27$, $p < 0.05$), which is consistent with other studies. For instance, Dong et al. stated that the stand spatial structure affects regeneration through resource allocation [13]. In other words, the stand spatial structure acts on regeneration processes by regulating the allocation efficiency of key resources, including light, water, and nutrients. However, the direct effect of stand spatial structure showed opposite results on the *Larix gmelinii* forests in China's Greater Khingan mountains that mostly rely on negative regulation from non-spatial structure (e.g., stand volume per unit area, $\beta = -0.41$). In the case of the Qinghai spruce forest, the stand spatial structure promotes seedling establishment by increasing light and nutrient accessibility through greater canopy openness, consequently enhancing the regeneration density [22].

The positive effect of moss–litter thickness on regeneration density ($\beta = 0.26$) in our study contrasts with conventional understanding, which typically views thick litter as an obstacle to seed–soil interactions [45]. Moreover, some studies have demonstrated that needle litter inputs from *Picea* spp. can inhibit humus accumulation and slow decomposition rates under humid temperate conditions. However, this inhibitory effect is largely offset in the arid and cold Qilian Mountains. The thick moss–litter layer in our study area functions primarily as a water retention and thermal insulation layer rather than a physical or chemical inhibitor. Under severe water limitation and large diurnal temperature fluctuations, the microhabitat amelioration effect of moss–litter cover dominates over its decomposition-inhibiting effect. In our study, under the arid and semi-arid conditions of the Qilian mountains, the moss–litter thickness could have served both water retention and insulation effects, mitigating the stress of extreme temperatures on seedlings. This also aligns with observations from the other study, which suggests that “Qinghai spruce seedlings have higher survival rates in moss-covered areas” [21]. Additionally, the crown width (CW) shows a negative effect ($\beta = -0.22$), which is consistent with the study by Zhu et al. [12]. They were suggesting a “canopy competition inhibition hypothesis”, in which large tree expansion reduces resource availability for the understory.

4.4. Synergistic Effects of Multiple Factors on Regeneration Diversity

In our study, piecewise SEM accounted for 40% of the total variation in the regeneration morphometric diversity (HRCW), with positive effects of elevation ($\beta = 0.27$) and slope ($\beta = 0.20$) highlighting the role of topographic heterogeneity. Our result aligned well with the study by Li et al., who reported that “regeneration advantages on semi-shaded, lower slopes.” [46]. The complex terrain of the Qilian Mountains creates multiple microhabitats, further enhancing regeneration diversity. The negative effect of soil organic carbon ($\beta = -0.34$), however, contrasts with [13], who found that the “soil nutrients promoted *Larix gmelinii* regeneration morphometric diversity” in the Daxinganling Mountains, China, possibly due to increased sensitivity of Qinghai spruce to carbon-nitrogen ratio; high organic carbon, which may subsequently have led to nitrogen limitation, inhibiting species differentiation [13].

In our study, the competition index (CI) indirectly promoted regeneration diversity by enhancing moss–litter thickness development ($\beta = 0.21$). Specifically, the piecewise SEM demonstrated that CI exerted a direct positive effect on moss–litter thickness (MLT, $\beta = 0.37$, $p < 0.001$) and an indirect inhibitory effect on soil organic carbon (OC) accumulation ($\beta = -0.18$, $p = 0.004$), while MLT and OC also exhibited a significant covariance relationship ($r = 0.18$, $p = 0.019$), suggesting shared ecological processes between them. This cascade relationship reflects that moderate competition among moss–litter thickness, regulated by CI, modulates microenvironments (e.g., water retention and temperature insulation) through adjusting MLT, thereby indirectly facilitating the differentiation of regeneration individuals and promoting regeneration diversity. This result is similar to the “terrain-stand structure-soil and water conservation function” relationship model developed by Wei et al. [47], where terrain factors affect soil and water conservation functions to a certain extent by influencing the stand structure.

The positive effect of the leaf area index (LAI, $\beta = 0.21$) in our study indicates that moderate canopy closure in Qinghai spruce forests (mean LAI = 1.34, range 0.44–1.63; Table 2) balances light and humidity, as shown by the significant positive path from LAI to regeneration diversity in the piecewise SEM (Figure 6). Our result is consistent with the study by He et al. [48], who suggested that “regeneration diversity has a unimodal relationship with canopy gap size”, as the gap size modulates microenvironmental factors including light availability and soil moisture regime, thereby inducing a unimodal pattern in regeneration diversity along the gradient of small gaps (resource deficiency), moderate/large gaps (resource equilibrium), and extra-large gaps (resource imbalance). The peak of regeneration diversity occurs in moderate or large gaps with an area ranging from 50 to 120 m², whereas extra-large gaps show a decline in regeneration diversity due to excessive solar radiation and soil desiccation [48].

For Qinghai spruce forests in the Qilian Mountains, under conditions of moderate canopy density (mean canopy openness = 0.47, mean LAI = 1.34; Table 2), a continuous gradient of light and soil moisture is formed from the canopy layer to the understory, which is supported by the negative correlation between LAI and canopy gap fraction (VO) in the correlation matrix (Figure 3) and their reciprocal regulatory paths in the piecewise SEM (Figure 6). This gradient not only satisfies the shading requirements of shade-tolerant seedlings but also supplies adequate resources for light-demanding saplings, ultimately contributing to the peak of intraspecific regeneration diversity. This low explanatory power can be attributed to the high stochasticity of alpine ecosystems and the spatial patchiness of natural regeneration. This observed covariance indicates that unaccounted covariation exists between the two predictors within the model framework. This marginal trend implies that OC potentially exerts a significant negative influence on TD. In addition, indirect pathways amplified the inhibitory impact of CW, leading to differentiation between its direct and total effects on RD.

4.5. Management Implications and Study Limitations

Overall, moss–litter thickness (MLT), canopy openness (B), and organic carbon (OC) are identified as core factors controlling Qinghai spruce regeneration. Based on our results, it is recommended to adopt ecological tending thinning combined with scientific preservation of the moss–litter thickness within the framework of the reserve’s management guidelines and following special ecological assessments and approvals. Specifically, low-intensity ecological tending thinning (non-commercial logging) should be implemented to increase the canopy’s openness to 0.5–0.6 (current average: 0.47). This measure refers to the technical method “optimizing stand structure through ecological tending” [49–51], with strict control over thinning intensity ($\leq 15\%$), scope (avoiding core protected areas), and targets (only removing diseased, weak, and overcrowded trees). A 5–6 cm

moss–litter thickness should be preserved to maintain soil water retention capacity, while tending measures should be taken to prevent physical barriers to seed colonization caused by excessively thick moss–litter thickness (>10 cm). All operations must comply with the ecological protection regulations of the Qilian Mountains National Nature Reserve and be implemented following special approval by forestry authorities and expert demonstration, with post-operation ecological monitoring and effectiveness evaluation conducted to verify outcomes.

This study has two major limitations: (1) All sampling microplots were confined to the geographically constrained Dayekou watershed, meaning the detected regeneration patterns cannot comprehensively reflect the broad ecological heterogeneity across the full Qilian Mountains range. Spatial autocorrelation diagnostics further confirmed substantial fine-scale microhabitat variability within the study domain, while no significant distance-dependent spatial structuring was observed across sampling units. Such prominent within-watershed microscale divergence implies that ecological heterogeneity would be drastically amplified when extrapolating the present findings to the mountain-wide landscape scale. (2) Seed rain dynamics and animal-mediated seed dispersal processes were excluded from our analytical framework, mandating prudent interpretation of all results reported in this study. Zhang Lingyu's research indicates that seed dispersal should be made a key precondition for regeneration studies in cold-temperate coniferous forests [52]. Future studies should integrate remote sensing and seed-tracking techniques to improve understanding of the driving mechanisms of the Qinghai forests' regeneration.

5. Conclusions

Moss–litter thickness, altitude, soil organic carbon, and crown width were identified as the common controlling factors for both regeneration indices. Canopy openness-driven stand structure, moss–herb interaction of ground cover, and terrain–soil coupling jointly dominate the natural regeneration process.

Distinct from temperate coniferous forests, the moss–litter layer within this alpine arid ecosystem primarily functions as a water-retention and thermal-insulation medium to facilitate seedling natural regeneration. As elaborated in Section 4.4 of the Discussion, elevated SOC concentrations constrain morphometric differentiation of regenerated seedlings; specifically, higher SOC levels correspond to diminished seedling morphometric diversity. The thresholds of canopy openness (0.5–0.6) and moss–litter thickness (5–6 cm) derived from this model could serve as tentative reference values for ecological restoration and refined management of alpine forests. Given the relatively low explanatory power of the regeneration density model and the strong stochasticity of alpine ecosystems, these values are regarded as model-based inferences rather than definitive prescriptions. Accordingly, protecting the original moss–litter ground cover is recommended to help maintain favorable seedling microhabitats and natural regeneration potential, in combination with the above model-derived reference thresholds.

Because of the limited sampling coverage, absence of seed rain and animal dispersal effects in this study, caution should be taken while interpreting the results. Future research shall expand sampling coverage across the Qilian Mountains to further validate the applicability of these model-inferred thresholds. Integrating seed tracking, remote sensing techniques, and freeze–thaw meteorological factors will also help to systematically clarify the multi-factor regulation mechanism of alpine forest regeneration.

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Data Availability Statement: Raw data supporting the conclusions of this study will be made available by the authors, without undue reservation.

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Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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