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Elevation-Dependent Natural Regeneration of *Abies georgei* var. *smithii* Forest in Southeastern Tibet

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Abstract: The comprehensive impacts of biotic and abiotic factors on the natural regeneration of *Abies georgei* var. *smithii* (*Abies*) forests in Tibet are not thoroughly understood. To address this gap, our study focused on the regeneration densities of *Abies* seedlings, saplings, and small trees across 21 plots (each 20 m × 20 m) along an elevation gradient from 3730 m to 4330 m in the Sygera Mountains of Southeastern Tibet. We meticulously measured a suite of 11 variables that describe stand structures and ecological conditions. Through analyses using Spearman's correlation analysis, hierarchical partitioning, and multiple linear regression, we identified key ecological drivers for successful *Abies* regeneration. Our results highlighted a peak in the abundance of seedlings, saplings, and small trees at an elevation of 3930 m. As the elevation rose from 3730 m to 4330 m, we observed an initial increase followed by a decrease in canopy cover (canopy), mother tree density (MotherT), 1000-seed weight (SeedW), litter thickness (LitterT), moss cover (MossC), moss thickness (MossT), soil moisture (SM), and soil bulk density, while mean annual temperature and soil depth to permafrost consistently decreased. The critical ecological drivers for *Abies* natural regeneration were identified as follows: MossT was pivotal for seedling density; canopy and MossC were influential for sapling density, and MotherT was the main factor affecting the density of small trees. This study suggests that a high density of mother trees and a thick and highly covered layer of moss are conducive to the natural regeneration of *Abies* in the Sygera Mountains. Understanding the current status of regeneration is vital for informing conservation and management strategies for *Abies* forests in Tibet.

Keywords: ecological factor; elevation; forest stand; natural regeneration; moss; Tibet

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1. Introduction

Natural regeneration—the ongoing cycle of plant species or communities arising from seed maturation, dispersion into the soil, seedling emergence, and growth, culminating in the formation of a healthy individual—is a critical component in the establishment of complex structures and diverse species assemblies in communities, including trees, shrubs, and herbs. This process is a fundamental mechanism for creating multilayered structures and rich species composition [1]. Forest natural regeneration is of paramount importance for the substitution of senescent trees with juvenile ones, ensuring both spatial and temporal consistency in forest ecosystems. It is essential for the progression of forest succession, sustainable development, and the preservation of forest health [2–4]. Extensive research has examined regenerated seedlings and the factors that affect their distribution, growth, and survival rates [5–8], highlighting that seedlings represent the principal method of forest propagation and ecological succession. Additionally, saplings and smaller trees constitute significant reserves for future forest rejuvenation, shaping the trajectory of future community dynamics [1,9–11]. Consequently, a comprehensive analysis of seedlings, saplings, and small trees is vital for a thorough understanding of the natural regeneration patterns of a particular tree species.

Abies georgei var. *smithi* (Viguié & Gaussen) W. C. Cheng & L. K. Fu (hereafter referred to as *Abies*) stands as a forest type of considerable ecological significance endemic to China. Its range spans Southwest Sichuan, Northwest Yunnan, and Southeastern Tibet, where it occupies a strategic ecological niche within the environmental security shield of Tibet, offering tourism and economic values [12]. As the predominant climax species within the dark coniferous forests of the Sygera Mountains in Southeastern Tibet, *Abies* thrives despite the challenges of intense solar radiation, persistent low temperatures, and significant snow coverage [13]. Research indicates that the severe conditions of the Sygera Mountains impede *Abies* seedlings' expansion at higher elevations, with deforestation and habitat destruction further curtailing their growth opportunities [14]. *Abies* generate abundant seeds roughly triennially; however, this does not ensure successful natural regeneration [15]. The absence of young trees in the natural regeneration cycle has led to population aging and decline, posing a substantial threat to their stability and sustainability [14]. Time-series predictions warn of an intensifying aging trend within the *Abies* population and a consequent decline [13]. These findings highlight the challenging regeneration prospects of the *Abies* forests in the Sygera Mountains.

Comprehending the elements that shape forest natural regeneration is a critical research focus for forest practitioners and conservators [2]. This regeneration hinges on the inherent capacity of ecosystems for self-recovery, representing a multifaceted interplay of ecological factors. The interrelated dynamics of biotic and abiotic components—ranging from canopy and underbrush vegetation, stand and site conditions, and soil characteristics—to various disturbances are recognized as influencing forest regeneration both directly and indirectly [5,16–21]. Tree species across diverse forest habitats and regions exhibit complex regenerative behaviors in response to these variables [22,23]. The impacts of these factors are pivotal, altering resource availability and environmental conditions essential for the emergence, growth, and persistence of seedlings, saplings, and small trees [24]. Nonetheless, the specific ways in which biotic and abiotic factors determine the regeneration patterns of *Abies* in Tibet remain insufficiently elucidated.

Prior research has frequently overlooked the influence of elevation on the distribution of *Abies*, partly because of its relatively narrow altitudinal range (3550–4350 m) in the Sygera Mountains. In this study, we examined the population dynamics of *Abies*, focusing on seedlings, saplings, and small trees, across an elevational gradient spanning 3730 m to 4330 m, along with ten additional influencing factors. Our investigation sought to address the following questions: (1) What is the pattern of natural regeneration for *Abies* across the elevation gradient? (2) How do the eleven identified factors impact the regeneration processes of *Abies*, including its seedlings, saplings, and small trees? (3) What role do mosses play in the natural regeneration of *Abies*? The insights gained from this study are intended to inform the development of nuanced artificial management strategies, thereby facilitating the ongoing stability and sustainability of *Abies* forests.

2. Materials and Methods

2.1. Study Area

This study took place in the shadowy expanse of the Sygera Mountains' dark coniferous forests, located in Nyingchi County, Tibet (94°25′–94°45′ E, 29°35′–29°57′ N). Elevation within the Sygera Mountains sweeps from 2100 m to a soaring 5300 m, and the area of *Abies* distribution is observed between 3550 m and 4350 m. The mountain climate is characteristically humid, emblematic of the subalpine, cold temperate zone. Influenced by the Yarlung Zangbo River's corridor of water vapor and the Indian Ocean monsoon, the region enjoys a temperate winter and a cool summer, with sharply delineated wet and dry seasons. Average annual air temperatures hover between 2.0 °C and 4.5 °C, plummeting to a chilling −4.1 °C in the coldest month and cresting at a mild 11.1 °C in the warmest. Yearly rainfall totals span a range of 875 mm to 1350 mm, the bulk of which—88%—descends from April through September. With an annual evaporation rate of 601 mm and an average humidity of 83%, the region's soil is predominantly acidic brown, with a pH ranging from 4 to 6. It features a robust soil layer distinctly rich in humus [25]. Vegetation transitions from spruce forests at lower elevations to fir and rhododendron mixed forests and then to higher altitudes featuring alpine willow and square branch forests; dark coniferous woods dominated by *Abies*; and finally, to alpine scrubs and meadows [26].

2.2. Sampling and Data Collection

In 2008, a trio of 20 m × 20 m permanent plots were established at 100 m intervals along the elevation gradient of the Sygera Mountains' eastern slope, ranging from 3730 m to 4330 m. A decade later, in October 2019, these plots were the focus of detailed field surveys. For each plot, elevation, longitude, and latitude data were precisely recorded using a GPS receiver (model TX35-S300, Beijing Haifuda Technology Co., Ltd, Beijing, China). To assess the natural regeneration of *Abies*, an X-shaped sampling design was employed within each plot, where 5 subplots measuring 2 m × 2 m were designated (Figure 1), totaling 15 subplots at each elevation level and 105 subplots in the entire study area. Tree regeneration was classified into three stages according to the plant height and diameter at breast height (DBH): seedlings (height < 50 cm), saplings (50 cm ≤ height < 200 cm), and small trees (height ≥ 200 cm and DBH < 5 cm) [27,28].

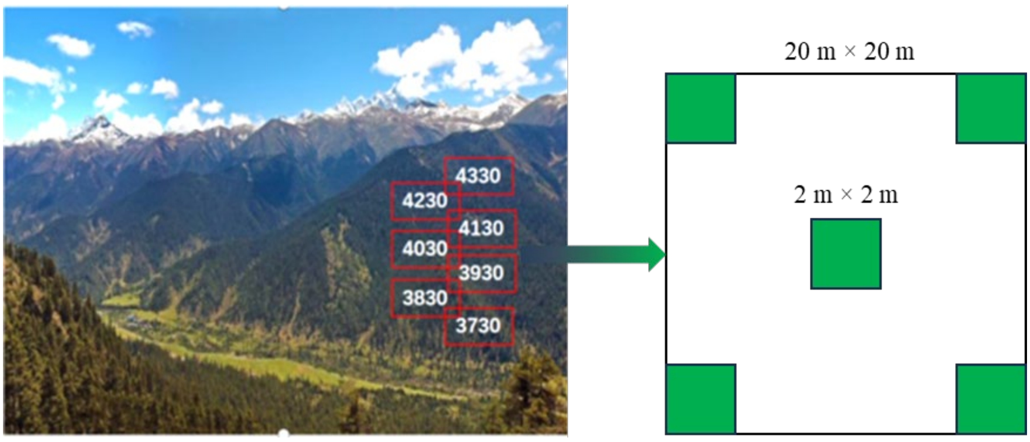

Figure 1. Sampling design along an elevation gradient of the Sygera Mountains' eastern slope. The red boxes in the left picture are the elevations where sample plots located.

The variables assessing forest stand structure included (1) the count, DBH, and height of all *Abies* encompassing seedlings, saplings, and small trees; (2) canopy cover (canopy); (3) density of mother trees (MotherT); and (4) the weight of 1000 seeds (SeedW). Seeds were collected from the eastern, western, southern, and northern vicinities of each mature tree. Following air-drying, SeedW was gauged by selecting and weighing three random samples of one hundred seeds each. Forest floor variables encompassed litter thickness (LitterT), moss thickness (MossT), and moss coverage (MossC). Soil characteristics included soil depth to permafrost (SPT), soil moisture (SM), and soil bulk density (SBD). Both SM and SBD were measured using a core sample, with surface litter and moss removed beforehand. The mean annual air temperature (MAT) was recorded utilizing an automatic meteorological sensor (RHT2nl-02, Vaisala, Helsinki, Finland). In sum, 11 ecological factors were taken into consideration to elucidate the spatial patterns of natural *Abies* regeneration—these factors included elevation, canopy, MotherT, SeedW, LitterT, MossT, MossC, SPT, SM, SBD, and MAT, tracking the early growth stages from seedlings to small trees.

2.3. Statistical Analysis

An analysis of variance (ANOVA) with the least significant difference (LSD) post hoc test was utilized to identify significant differences in the natural regeneration stages across various elevations, adopting a significance threshold of $p < 0.05$. A nonparametric Spearman's rank correlation was conducted to examine the interrelationships between the regeneration stages of seedlings, saplings, and small trees and the ecological factors, as well as the intercorrelations among ecological factors themselves.

Hierarchical partitioning [29] was chosen to gauge the discrete contributions of individual explanatory variables in the regeneration stages. These contributions' statistical significance was computed using randomization tests based on 100 permutations [30]. Multiple linear regressions were performed to discern the complex interplay between the young forest growth stages and their influencing ecological factors. Prior to the multiple linear regressions, variables exhibiting multicollinearity—with a variance inflation factor exceeding 10—were prudently removed. The best models were chosen based on the significance of explanatory variables and Adjusted R^2.

All statistical deliberations were executed in R version 4.3.1. The "hier.part" and "rand.hp" R packages enabled hierarchical partitioning and the corresponding randomization tests [31], respectively.

3. Results

3.1. Natural Regeneration Characteristics of Abies Forest in Relation to Elevation

From the 105 sampled subplots across an elevation gradient spanning 3730 m to 4330 m, we counted and measured 484 *Abies* in total, of which there were 254 seedlings, 116 saplings, and 69 small trees. Along this elevation gradient, the *Abies* regeneration stages—comprising seedlings, saplings, and small trees—exhibited strikingly similar unimodal distribution patterns. The densities of these stages showed a steady climb below 3930 m, culminating in density peaks at precisely 3930 m elevation. Beyond this point, there was a marked decline in densities, which dropped significantly as the elevation rose to 4330 m. The best-fitted curves of the stages to elevation showed that elevation significantly affected the densities of *Abies* seedlings, saplings, and small trees, with R^2 values reaching 0.717, 0.619, and 0.894, respectively (as depicted in Figure 2, $p < 0.001$).

At the peak density elevation of 3930 m, the populations of seedlings, saplings, and small trees were recorded at 48,000, 21,333, and 250 plants per hectometer squared (plant hm^{-2}), respectively. These figures were substantially greater than at nearly all other surveyed elevations ($p < 0.05$). This contrast was particularly stark when compared with the 4330 m elevation level, where the respective populations plummeted to 7333, 4666, and 50 plant hm^{-2}.

The outputs from the LSD tests revealed significant differences in the population densities across the various elevations for all three growth stages; these results underscored elevation as a crucial determinant influencing the natural regeneration processes of the *Abies* forest ($p < 0.05$).

3.2. Factors Influencing the Variations in Natural Regeneration of the Abies Forest

Table 1 presents the characteristics of 11 ecological variables across an elevation gradient from 3730 m to 4330 m. In this range, the values for Canop, MotherT, SeedW, LitterT, MossC, MossT, SM, and SBD first increased before subsequently declining, while MAT and SPT demonstrated a consistent decrease.

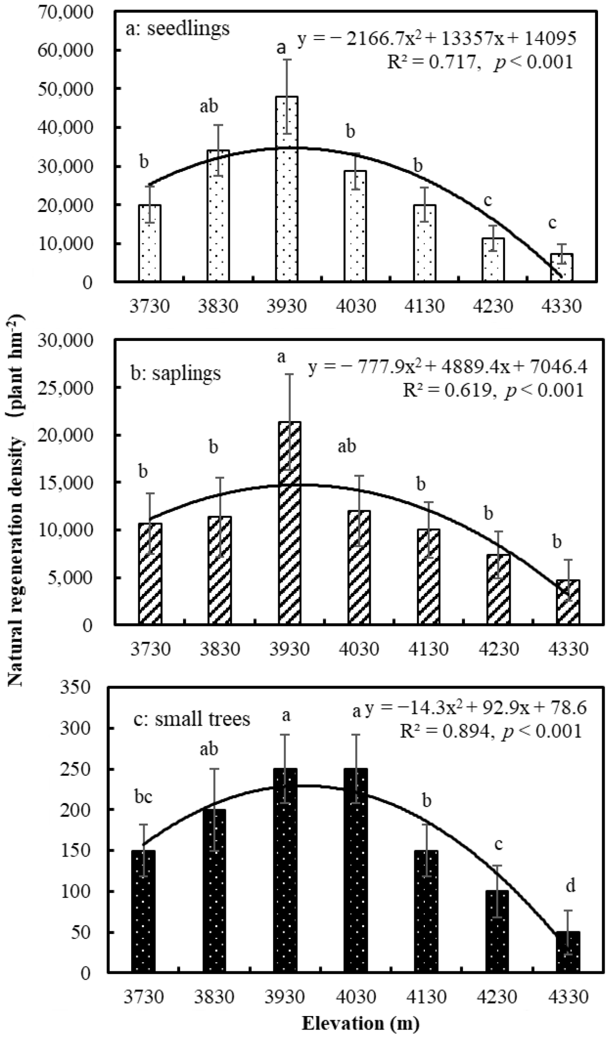

Figure 2. Densities of seedlings (**a**), saplings (**b**), and small trees (**c**) along an elevation gradient in the Sygera Mountains. Different lowercase letters mean significant differences between elevations at $p < 0.05$.

Table 1. Ecological conditions of *Abies* forest. Canopy: canopy cover, MotherT: mother tree density, SeedW: 1000-seed weight, LitterT: Litter thickness, MossC: moss cover, MossT: moss thickness, SM: soil moisture, SBD: soil bulk density, MAT: mean annual air temperature, SPT: soil thickness from surface to permafrost. Different lowercase letters indicate significant differences at $p < 0.05$.

Elevation m	Canopy %	MotherT Plant hm^{-2}	SeedW g	LitterT cm	MossC %	MossT cm	SPT cm	SM %	SBD g cm^{-3}	MAT °C
3730	69.40 ± 2.43 a	600 ± 25 ab	10.31 ± 0.16 c	8.38 ± 0.33 a	45.08 ± 6.49 ab	5.21 ± 0.700 a	11.32 ± 0.19 a	39.41 ± 2.37 a	0.58 ± 0.03 b	−0.46 ± 0.03 a
3830	63.00 ± 3.56 a	800 ± 85 a	12.34 ± 0.19 a	8.56 ± 0.26 a	53.67 ± 6.55 a	6.63 ± 0.90 a	10.45 ± 0.28 b	44.3 ± 1.01 a	0.74 ± 0.02 a	−1.16 ± 0.05 b
3930	70.61 ± 2.30 a	900 ± 51 a	11.35 ± 0.13 b	8.49 ± 0.28 a	46.27 ± 6.95 a	6.70 ± 0.86 a	9.97 ± 0.33 b	40.52 ± 2.16 a	0.72 ± 0.04 a	−1.70 ± 0.07 c
4030	50.00 ± 3.20 b	800 ± 52 a	9.64 ± 0.12 c	4.87 ± 0.20 b	35.80 ± 6.70 b	4.65 ± 0.65 ab	9.06 ± 0.36 c	37.74 ± 0.98 a	0.80 ± 0.03 a	−2.32 ± 0.17 d
4130	49.50 ± 3.67 b	700 ± 42 a	8.53 ± 0.26 d	4.41 ± 0.28 b	32.07 ± 6.53 b	3.79 ± 0.68 b	8.57 ± 0.36 c	38.73 ± 0.56 a	0.86 ± 0.01 a	−2.95 ± 0.47 e
4230	40.00 ± 2.69 c	500 ± 34 b	7.70 ± 0.28 d	3.36 ± 0.21 c	24.33 ± 3.92 bc	3.59 ± 0.80 bc	7.35 ± 0.29 d	37.76 ± 0.62 a	0.78 ± 0.02 a	−3.59 ± 0.18 f
4330	18.00 ± 1.26 d	200 ± 17 b	6.67 ± 0.40 e	2.70 ± 0.21 c	15.20 ± 2.65 c	2.12 ± 0.44 c	5.91 ± 0.24 e	24.82 ± 2.76 b	0.70 ± 0.03 a	−4.22 ± 0.27 g
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Specifically, at the highest elevation of 4330 m, SeedW, LitterT, MossC, and SM showed their lowest values (6.67 g, 2.70 cm, 15.20%, and 24.82%, respectively), while their highest values (53.67 g, 8.56 cm, 44.3%, and 12.34%, respectively) were at a 3830 m elevation. Canopy, MotherT, and MossT also hit their lowest at 4330 m (18.00%, 200 plants hm^{-2}, and 2.12 cm, respectively), with their maxima observed at 3930 m (6.70 cm, 70.61%, and 900 plants per hectometer square, respectively). SBD was at its minimum (0.58 g cm^{-3}) at the lowest elevation of 3730 m and reached a peak (0.86 g cm^{-3}) at 4130 m. Statistically significant variations were evident across these factors along the elevation gradient ($p < 0.001$).

The outcomes of Spearman's correlation analysis, depicted in Figure 3, illustrate the correlations between the *Abies*' regeneration stages (seedlings, saplings, and small trees) and various ecological factors, as well as the correlations among the ecological variables themselves. Seedlings displayed a high correlation with MossC, MossT, MotherT, and SeedW ($r > 0.68$, $p < 0.01$) and a significant correlation with canopy, LitterT, and elevation ($p < 0.05$). Saplings displayed significant correlations with canopy, LitterT, SPT, and SM ($p < 0.05$). Small trees showed correlations with almost all ecological variables ($p < 0.05$) except SBD, in which MotherT, SeedW, and LitterT showed high correlations ($r > 0.57$, $p < 0.01$).

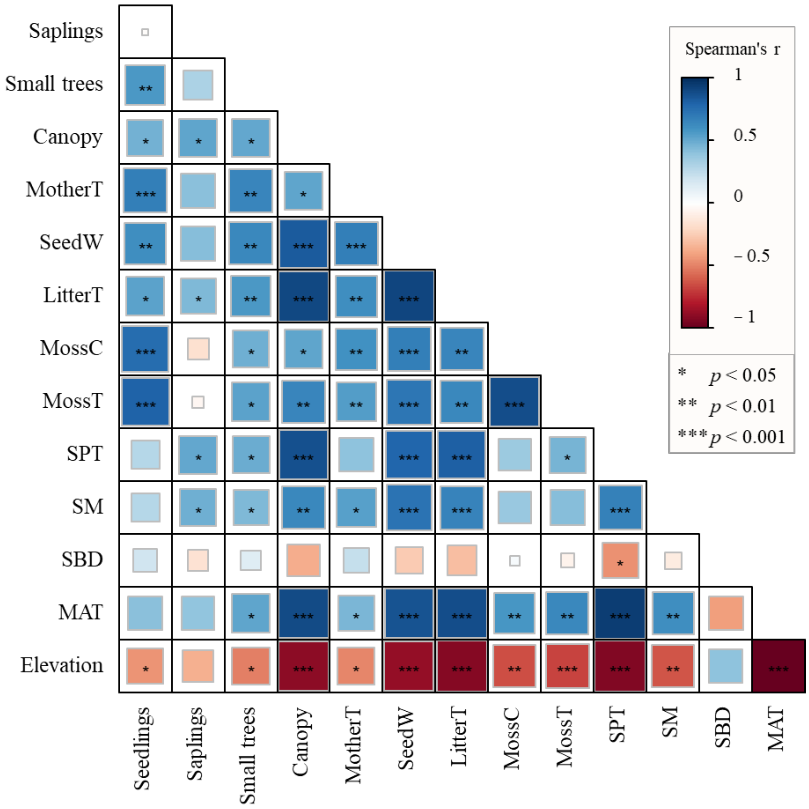

Figure 3. Relationship of the natural regeneration of the *Abies* forest to ecological factors via Spearman's correlation analysis. Pairwise correlations of ecological factors are shown, with a color gradient denoting Spearman's correlation coefficient.

Among ecological factors, elevation was found to have a strong negative correlation with SPT, LitterT, SeedW, and canopy ($r > 0.85$, $p < 0.001$). In contrast, MAT presented exactly the opposite correlations with these factors, due to a very high negative correlation between elevation and MAT ($r = 0.99$, $p < 0.001$). Furthermore, canopy with LitterT; canopy and SPT; Litter and SeedW, and MossC and MossT demonstrated strong positive correlations with one another ($r > 0.85$, $p < 0.001$).

Hierarchical partitioning analysis was employed to discern the primary causal variable from the aforementioned ecological factors that influence the natural regeneration of *Abies* forests while concurrently addressing the issue of multicollinearity among multiple variables. The isolated effects of each independent variable are illustrated in Figure 4.

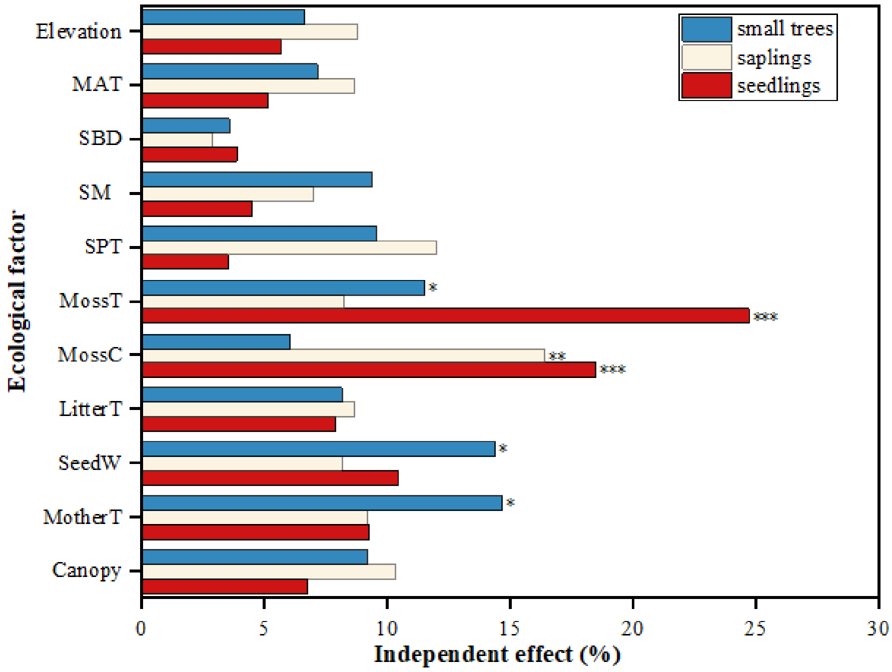

Figure 4. Hierarchical partitioning of ecological factors explaining the seedlings, saplings, and small trees of *Abies* in Southeastern Tibet. The significance of the independent contributions of each variable is indicated. *** significant at $p < 0.001$, ** significant at $p < 0.01$, and * significant at $p < 0.05$.

MossT emerged as the dominant factor affecting seedling abundance, accounting for 24.69% of the observed variance ($p < 0.001$). MossC was also a significant contributor, explaining 18.49% of the variation ($p < 0.001$). For saplings, MossC again proved to be the most impactful, representing 16.39% of the variance ($p < 0.01$). Successive factors included SPT and canopy, contributing 11.95% and 10.28%, respectively. Regarding small trees, the chief contributing factors were MotherT, SeedW, and MossT, which accounted for 14.68%, 14.37%, and 11.50% of the variance, respectively ($p < 0.05$).

Multiple linear regression analyses provided a detailed understanding of how ecological factors influence the natural regeneration of *Abies*, as shown in Table 2. Seedling presence was most effectively predicted by MossT, accounting for 67.5% of the variation ($R^2 = 0.675$, $p < 0.05$). The occurrence of saplings was best predicted by a combination of canopy and MossC, which collectively accounted for 61.2% of the variance ($R^2 = 0.612$, $p < 0.05$). As for small trees, their distribution was largely explained by MotherT, explaining 45.1% of the total variation ($R^2 = 0.451$, $p < 0.05$).

Table 2. Multiple linear regressions of natural regenerations of *Abies* (seedlings, saplings, and small trees) with ecological factors.

Whole Model	Variable	Seedlings		Saplings		Small Trees	
		t	*p*	t	*p*	t	*p*
	Constant	−0.907	0.382	0.513	0.617	−1.211	0.249
	Canopy	0.575	0.576	2.275	0.042	−0.479	0.640
	MotherT	0.732	0.478	1.847	0.089	1.058	0.311
	SeedW	1.022	0.327	1.844	0.090	0.726	0.482
	MossC	−0.113	0.912	−3.434	0.005	−0.802	0.438
	MossT	2.285	0.041	−0.244	0.811	1.356	0.200
	SPT	0.274	0.789	−0.951	0.361	1.171	0.264
	SM	−2.238	0.045	−1.353	0.201	−0.773	0.454
	BD	1.707	0.114	−0.122	0.905	1.065	0.308

Table 2. *Cont.*

Whole Model	Variable	Seedlings		Saplings		Small Trees	
		t	p	t	p	t	p
Model statistics							
R^2		0.810		0.799		0.648	
Adjusted R^2		0.683		0.665		0.413	
F		6.386		5.962		2.756	
p		0.002		0.003		0.055	
Best Model	Variable	t	*p*	t	*p*	t	*p*
	Constant	−1.848	0.080	0.052	0.959	0.376	0.711
	Canopy			5.540	0.000	4.172	0.001
	MotherT						
	MossC			−4.526	0.000		
	MossT	6.528	0.000				
Model statistics							
R^2		0.692		0.651		0.478	
Adjusted R^2		0.675		0.612		0.451	
F		42.617		16.771		17.405	
p		0.000		0.000		0.001	

4. Discussion

4.1. Effects of Forest Stand Structure Factors on Natural Regeneration of Abies

The forest stand structure has a demonstrable predictive impact on the natural regeneration of *Abies* species. Existing research indicates that optimal regeneration density occurs when the canopy cover is between 0.60 and 0.65. Conversely, a canopy cover greater than 0.70 tends to be detrimental, as the growth of seedlings and saplings is hindered by a lack of sufficient light [32]. *Abies*, being a shade-tolerant species, nonetheless requires a degree of shading during its seedling stage for optimal growth [33]. Environments with high canopies not only furnish moderate light levels suitable for seed germination but also provide the necessary shading conditions for the survival of *Abies* seedlings. As natural regeneration progresses, there is an increased demand for light and other resources, which makes the formerly conducive shaded conditions less capable of satisfying light requirements during the transition to the small-tree stage [34–36]. In this study, a positive correlation ($p < 0.05$) was found between stand canopy cover and the presence of the three regeneration stages of seedlings, saplings, and small trees. Even though the independent effect of the canopy cover on seedlings (6.72%), saplings (10.28%), and small trees (9.16%) was not significant, it was identified as an efficient predictor for the growth of saplings via stepwise regression.

The mother tree, a critical determinant of seed quantity and quality, serves as a fundamental measure of a forest stand's reproductive potential [9]. It also affects the canopy light conditions, litter thickness, and soil moisture levels, with increasing stand density typically resulting in thicker litter layers but reduced soil moisture and light penetration [37,38]. Consequently, mother tree density can exert multifaceted environmental influences on progeny. In the sample plots of the study area, the canopy only consisted of mother trees of *Abies*, and the mother tree density exhibited high correlations with seed weight, as well as the natural regeneration stages of seedlings and small trees ($r > 0.65$, $p < 0.01$). It was also found to have a significant independent effect on small trees ($p < 0.05$) and was consistently identified as an exclusive and positive contributing factor in the multiple regression analysis for small trees within this ecological context. These findings suggest that, in the study area, the *Abies* mother trees maintain relatively high seed quality despite challenging environmental conditions, and their density is not so great as to impede the growth of their regenerates. This low-to-medium density (200–900 plants hm^{-2}) and cover (18%–70%) of stands were somehow beneficial with regard to the natural regeneration of *Abies*. This result is aligned with findings from related research [24,39,40].

4.2. Effects of Forest Floor Attributes on Natural Regeneration of *Abies*

Forest floor attributes, encompassing the attributes of the litter and moss layer, play important roles in regulating the natural regeneration of *Abies* forests. The litter layer on forest floors is a pivotal element influencing the natural regeneration process. The presence and thickness of litter serve multiple roles, providing shade, retaining moisture, offering insulation, and presenting mechanical barriers, all of which have complex and dualistic impacts on seed germination, as well as the establishment, growth, and development of seedlings [32,41,42]. The presence of seedlings, saplings, and small trees of *Abies* was found to have a significant positive correlation with LitterT ($p < 0.05$). However, litter thickness independently exerted non-significant effects on the various stages of natural regeneration ($p > 0.05$). Thus, litter thickness emerges as a less important factor that facilitates the natural regeneration of *Abies* in Southeastern Tibet.

Moss constitutes a vital component of the *Abies* forest floor ecology, acting as a key interface for water vapor exchange within forest ecosystems. It significantly shapes the natural regeneration dynamics of *Abies* species [1]. Studies indicate that the effects of moss on forest regeneration, whether supportive or inhibitory, are largely contingent upon the moss layer's thickness and moisture content [9,43]. In the scope of this study, the thickness and coverage of the moss layer were found to be pivotal in the emergence of seedlings. While moss coverage was observed to positively influence seedling emergence, it adversely affected sapling development. Moss layers provide a protective barrier against foraging animals, potentially increasing the preservation of *Abies* seed banks. Additionally, the inherent water retention capabilities of moss layers offer crucial hydration, facilitating seed germination and seedling growth [44,45]. As *Abies* individuals progress from seedlings to saplings, their requirements for water and nutrients escalate, needs that a dense moss layer may inadequately meet. Oftentimes, excessively thick moss layers can also result in reduced nutrients reaching the plants. As a result, saplings may experience drought conditions and inadequate nutrients that can lead to high mortality rates [39,44,46].

4.3. Effects of Abiotic Factors on Natural Regeneration of *Abies*

Abiotic factors, including topography, climate, and soil properties, play a critical role in the natural regeneration processes of *Abies* species. The influence of topography—and elevation in particular—is notable, as it modifies plant growth conditions and affects the natural forest vegetation's vertical distribution, thereby impacting forest regeneration [24,47]. Elevation significantly alters factors such as temperature, humidity, and light availability, which can influence natural regeneration processes. These alterations can lead to changes in forest stand structure and microclimates, ultimately affecting seed germination rates and the emergence of seedlings.

This study found that, with increasing elevation, the density of *Abies* regeneration exhibits a unimodal distribution, with a peak at 3930 m above sea level. Furthermore, elevation was determined to have a significant impact on the occurrence of seedlings, saplings, and small trees ($p < 0.001$). The average elevation of the study sites is around 4000 m, where MAT typically falls below 0 °C (refer to Table 1). At such low temperatures, the soil often remains frozen, posing challenges for seedlings, saplings, and small trees, as it impairs their ability to absorb water, inhibiting growth and potentially leading to death because of physiological drought conditions. Despite *Abies*'s adaptability to cold and alpine environments, natural regeneration is less effective at higher elevations compared with lower ones. This indicates that cold temperatures and associated conditions at high altitudes pose constraints on the successful natural regeneration of this cold-tolerant alpine tree species.

Topography plays a crucial role in both the accumulation and dispersal of soil nutrients, which, in turn, indirectly influences plant distribution [24]. Research has demonstrated that changes in the landscape can significantly affect soil physical and chemical characteristics, as well as moisture dynamics [48,49]. Furthermore, stands with low-to-medium density appear to exhibit superior chemical soil properties such as higher levels of soil organic matter, total phosphorus, available phosphorus, and nitrogen and better physical properties like increased noncapillary pore space and optimal water-holding capacity [39]. It has been established that soil nutrients, including soil organic matter, total nitrogen, available phosphorus, and potassium, play a significant role in vegetative growth and development [24,39]. In the current study, while soil nutrients were not directly addressed, physical soil properties such as SPT, SBD, and SM were considered. These factors influenced the viability of *Abies* regenerates, with SPT and SM showing a significant correlation with the survival of saplings and small trees ($p < 0.05$). However, they did not show up as significant independent factors or effective predictors in the multiple regressions. This indicates that physical soil properties have fewer effects than forest stand and floor attributes on the regeneration of *Abies* forest.

5. Conclusions

This research offers a thorough analysis of the ecological factors that influence the natural regeneration of *Abies* on the high-altitude Southern Tibetan Plateau. Regeneration in terms of seedlings, saplings, and small trees showed a strong dependency on elevation, with the highest abundance observed at an elevation of 3930 m. Distinct ecological factors were found to influence the natural regeneration of *Abies* at different stages of development. Within the 11 ecological factors, the biotic factors, including forest stand structure and floor attributes (especially moss layer), emerged as more effective variables than abiotic factors, such as soil properties and MAT. The presence of seedlings was primarily determined by moss thickness (MossT); sapling growth was influenced by canopy cover (canopy) and moss coverage (MossC); and the growth of small trees was dictated by mother tree density (MotherT). These findings indicate that the natural regeneration of *Abies* benefits from conditions such as a high density of mother trees and canopy cover and substantial moss coverage and thickness. These results offer valuable insights for conservation and management efforts regarding *Abies* forests in Tibet, informing strategies for preserving this key species within its native habitat.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15010142/s1, Table S1: Variables assessing forest stand structure.

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