

Article

Relationship Between Climate Changes and Forest Dynamics Along Altitudinal Gradients at Doi Suthep-Pui National Park, Northern Thailand

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Abstract: Climate change has become a prominent topic, particularly regarding plant adaptation and migration within mountain ecosystems. This study aimed to clarify forest dynamics by focusing on sapling and tree stages in relation to microclimate changes across a permanent plot along an altitudinal gradient. In 2012, a permanent transect plot (50 m × 600 m) was established at the forest ecotone between the deciduous dipterocarp forest (DDF) and lower montane forest (LMF). All trees with a diameter at breast height ≥ 1 cm were tagged, measured, and identified. Monitoring occurred every 2 years between 2012, 2014, 2016, and 2018, with a final census conducted in 2023. Microclimatic factors were recorded automatically, and rainfall data were obtained from a meteorological station. The dynamics of all trees were analyzed in relation to micro-climate changes. Our results showed that environmental changes significantly affected species coexistence, particularly in the forest ecotone between the DDF and LMF, where intermediate environmental factors were observed. High mortality rates were observed in the dominant evergreen species, with significant positive correlations with decreased rainfall and increased temperature, suggesting that drought conditions strongly influence tree mortality. In contrast, the deciduous species showed increased density, particularly in the forest ecotone zone, indicating their better adaptation to drought conditions and their potential to occupy the forest ecotone at a higher rate than LMF species. Understanding the ecological niches of coexisting species along altitudinal gradients is crucial for developing effective restoration programs in mountainous ecosystems.

Keywords: climate change; coexisting tree species; drought conditions; ecological niche; environmental gradient; forest dynamics; mountain ecosystems



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1. Introduction

Global environmental issues, such as land-use changes and biodiversity losses, are central to humanity's grand challenges [1–3], particularly with the ongoing expansion of agricultural areas [2]. Forest loss and degradation contribute substantially to climate-warming gas emissions and place at least 8% of forest plants and 5% of forest animals at an extremely high risk of extinction [4–6]. Establishing native forest plantations on degraded agricultural land is an effective strategy for promoting biodiversity conservation and forest recovery [7,8]. However, assessing the recovery process and its success requires long-term evaluation. Long-term ecological research (LTER) is an important approach to understanding forest dynamics in response to various disturbances [9,10]. The use of permanent plots plays a vital role in detecting ecosystem responses, particularly those related to specific environmental changes [11–13].

Many ecosystem changes, particularly those involving species or habitats, reflect region-specific environmental changes. To address these challenges, policymakers, environmental managers, and scientists need to detect environmental changes at multiple spatial and temporal scales through comprehensive biotic and abiotic research and monitoring programs [14,15].

LTER in Thailand also provided important ecological insights related to the interaction between forest regeneration and environmental factors, such as changes in forest recovery during successional stages, the dynamics of forest structure, and species composition [16–18]. Plant regeneration, particularly at the seedling and sapling stages, is highly sensitive to environmental changes, especially the effects of El Niño events in tropical seasonal forests [10,11,19]. Plants at these stages often suffer from high mortality owing to their sensitivity to environmental conditions and soil water shortages during severe droughts [20,21]. Recently, many researchers have reported that mountain ecosystems are ideal study areas for detecting the influence of environmental changes on tree regeneration dynamics, particularly along altitudinal gradients [11,21–23]. At the global scale, Vanderwel et al. reported on the relationship between geographic limits and different forest types based on prediction mode, suggesting that the observed climate sensitivity regarding mortality and recruitment in future vegetation distributions under climate change should be captured more appropriately [24]. Notably, temperature changes in mountainous regions over the past century have been more pronounced than those observed at the global or hemispheric scales. Consequently, the impacts of future climate change are expected to be more pronounced at higher elevations [6,25,26]. In addition, the ability of mountainous regions to provide essential goods and services to society is increasingly threatened by environmental changes [27,28]. Mountain ecosystems in northern Thailand primarily comprise evergreen and deciduous forest types [29,30], each of which often exhibits contrasting ecological adaptation strategies in its niche. The dominant forest types in mountain ecosystems are often distributed along altitudinal gradients. Montane forests, including lower and upper montane forests, occupy high elevations (1000 m above sea level [a.s.l.]), whereas deciduous dipterocarp forests (DDF) are found at lower than 900 m a.s.l. [31,32]. Deciduous species in the DDF are more drought-tolerant than evergreen species in the lower montane forest (LMF). The existence of a transition forest or forest ecotone (FEs) between the DDF and LMF (900–1100 m a.s.l.) may promote the coexistence of these forests owing to the intermediate environments in this area. Rapid environmental changes, particularly climate change, may influence plant regeneration [33] and coexisting species in various ecosystems, especially the combination of deciduous and evergreen species [32]. Increases in temperature and drought in the FE along altitudinal gradients affect the potential competition between deciduous and evergreen plants [34]. However, in-depth studies on topics such as how plant species adaptation and migration between these two forest types

are influenced by climate change are scarce. Thus, this study aimed to clarify the forest dynamics, particularly during the tree and sapling stages, related to microclimate changes in a forest dynamic plot (FDP) across the DDF and LMF at Doi Suthep-Pui National Park, Northern Thailand.

2. Materials and Methods

2.1. Study Area

The study area in Doi Suthep-Pui National Park is located at latitude $18^{\circ}43'30''$ – $19^{\circ}7'30''$ N and longitude $98^{\circ}48'20''$ – $98^{\circ}57'10''$ E in Chiang Mai Province, Thailand (Figure 1). Approximately 85% of the land cover is forest, and 15% consists of agricultural land and urban areas [35]. The Doi Suthep-Pui mountain ecosystem exhibits complex environmental factors, especially elevation gradients, which influence the distribution of forest types; these can be classified into deciduous forest (mixed deciduous and deciduous dipterocarp forest (DDF)), mostly found at low elevations of 312–900 m a.s.l., and evergreen forest (lower montane forest (LMF) and pine forest), mostly found at higher elevations (1000–1656 m a.s.l.) [30], as well as the forest ecotone area between the DDF and LMF, mostly at elevations between 900 and 1000 m a.s.l., where evergreen and deciduous species coexist, albeit only in a narrow zone where the environmental factors are similar to those of each forest (DDF and LMF) [19]. The area is characterized by a subtropical climate, featuring a long dry season alternating with a short wet season, an annual precipitation of 1139 mm, and a mean temperature of 24°C .

2.2. Data Collection

In 2012, a 1.8 ha permanent plot ($30 \times 600 \text{ m}^2$) was established across the FE between the DDF and LMF (latitude $18^{\circ}47'4''$ N, longitude $98^{\circ}54'58''$ E), where the elevation ranged from 900 to 1100 m a.s.l (Figure 1). The plot was expanded to 3 ha ($50 \times 600 \text{ m}^2$) in 2018. Each plot was divided into 300 subplots ($10 \times 10 \text{ m}^2$). Trees with a diameter at breast height (DBH) of greater than 1 cm were tagged, and their DBH was measured. Tree species were identified based on the criteria of Thai Forest Ecological Research Network (TFERN), Kasetsart University, Thailand. Monitoring was performed every 2 years (three times) between 2014, 2016, and 2018, followed by a fourth measurement at a 5-year interval in 2023.

The rainfall and rain-free days data were derived from the nearest weather station of Doi Suthep-Pui National Park ($18^{\circ}48'21''$ N, $98^{\circ}55'21''$ E, elevation: 1040 m a.s.l), located approximately 1200 m from the study's permanent plot. Temperatures were measured hourly throughout the monitoring of dynamics using 13 data loggers (HOBO UA-002-64, Onset Computers, Bourne, MA, USA) placed 1.3 m above the ground at 50 m intervals within the transect permanent plot.

2.3. Data Analysis

To investigate forest dynamics and how species associations change across life stages, these species were classified into two life stages: saplings (DBH > 1–4.5 cm) and adult trees (DBH > 4.5 cm). Tree dynamics were analyzed during each monitoring period every 2 years between 2012, 2014, 2016, and 2018, with a final census conducted in 2023. However, this analysis was conducted for each year of the tree census.

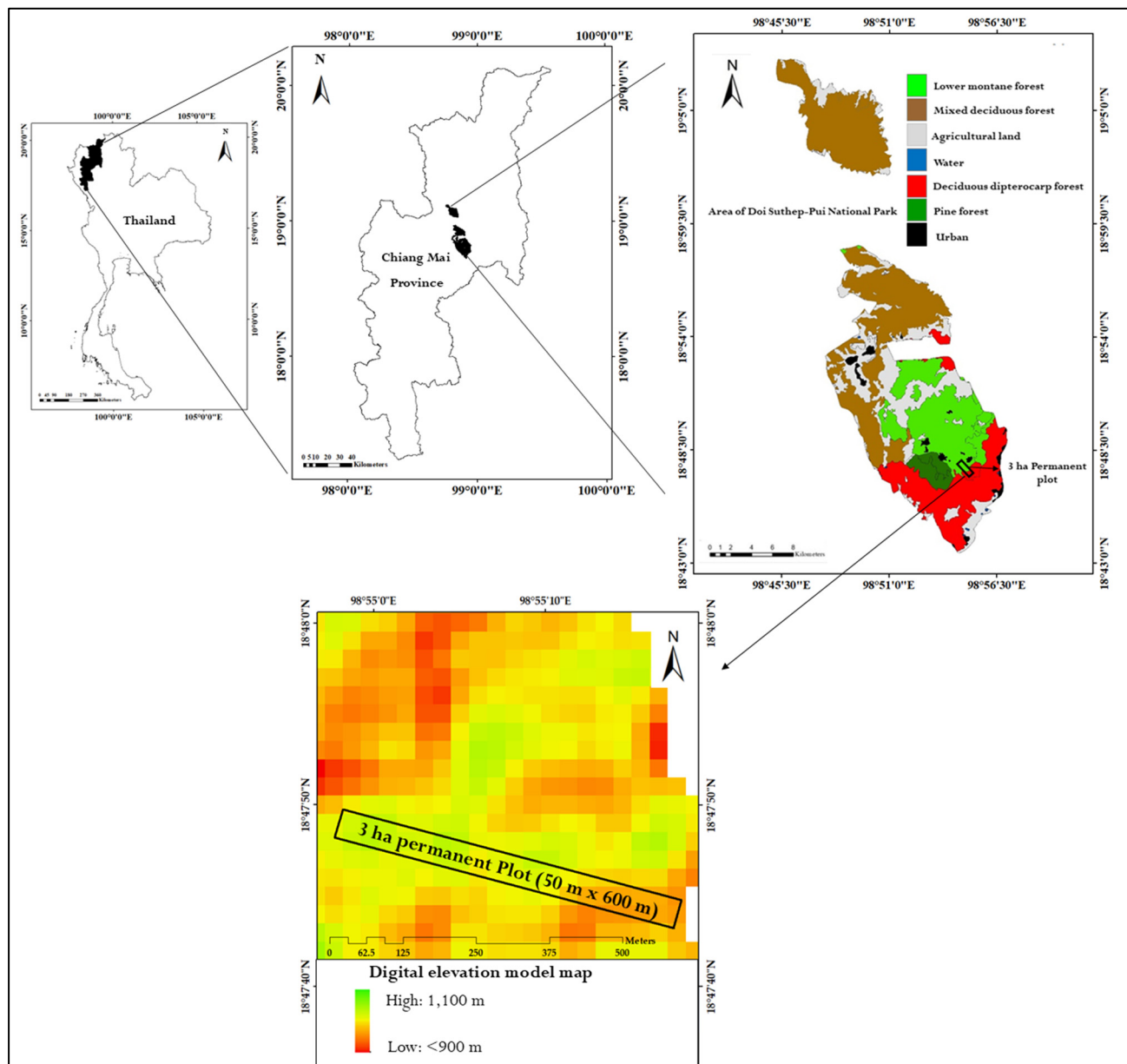


Figure 1. Doi Suthep-Pui National Park, Chiang Mai Province, Thailand, and the 3 ha permanent plot.

The number of dead and newly emerged trees in each period was analyzed using a one-way analysis of variance with a completely randomized design. The differences between periods were tested using Duncan's multiple range test (DMRT) in the R program.

Forest dynamics were characterized using annualized mortality (M) and recruitment (R), following the method of Sherman et al. [36], based on these equations:

$$M (\%) = 100 \times (\ln (N_0) - \ln (N_s)) / t$$

$$R (\%) = 100 \times (\ln (N_t) - \ln (N_s)) / t$$

where N_t and N_0 are the population numbers at time t and time 0, respectively, N_s is the number of survivors at time t , and $\ln$ is the natural logarithm. The relative growth rate (RGR) of tree species ($DBH \geq 4.5$ cm) was calculated using this equation:

$$RGR = (\ln (DBH_{t2}) - \ln (DBH_{t1})) / (t_2 - t_1)$$

where DBH is the diameter at breast height (1.3 m) of an individual tree at time $t_2 - t_1$ divided by the number of years between census periods.

The inverse distance weighting interpolation technique was used to map the microclimatic factors. All maps were analyzed using ArcMap version 10.1 [37,38]. The interpolation distribution technique estimates the values of different environmental factors (temperature and rainfall data) for each survey plot based on the geographic coordinates along the gradient to the center of the plot.

The relationship between forest dynamics and microclimatic factors was analyzed over all census periods, focusing on selected species with more than 100 individuals. A generalized linear model (GLM) was used to examine the relationships between environmental factors and tree dynamics. The dependent variables for each plot were the number of dead and new trees for each selected species, whereas the independent variables were the microclimatic factors. Independent variables were selected by calculating Pearson's correlation coefficients ($r \geq 0.80$ or $r \leq -0.80$) [39,40], which included five factors: annual mean temperature, light intensity, annual rainfall, rainy days, and soil moisture content. The model omitted two factors—rainy days and soil moisture content—because they are highly dependent on other environmental factors. Three factors were used to model the relationships between tree dynamics and microclimatic changes. The model with the lowest Akaike information criterion (AIC) was selected using stepwise AIC from the MASS package [41] available in R ver. 3.2.2 based on the following equation:

$$Y(I) = \text{glm}(\text{total number of trees dead or number of new trees (species } I) \sim x_1 + x_2 + \dots + x_6, \text{ family} = \text{gaussian (link} = \text{identity)}),$$

where x_1 and x_2 are the independent variables: x_1 is the annual mean temperature, while x_2 is the annual rainfall.

3. Results

3.1. Environmental Factors Data

Our results showed that microclimatic changes varied over the years. The average temperature during the 11-year period (2012–2023) was 27.69 ± 0.62 °C, while the mean annual rainfall was 1057.86 ± 190 mm/yr. Considering these changes, rainfall was lower in the period from 2018 to 2023 compared with the previous period (2012–2014), particularly in 2018 (the third monitored period). In contrast, the temperature increased by approximately 0.9 °C compared with the previous period. The years 2015–2016, 2018–2019, and 2023 were marked by El Niño events (Figure 2), as defined by the El Niño Southern Oscillation [42], which likely influenced the microclimate conditions in the study area. These climatic changes during the monitoring period may have contributed to shifts in forest dynamics, especially in the study area.

3.2. Forest Structure and Dynamics

Within the 3 ha permanent plot in 2023, 13,025 tagged trees ($\text{DBH} \geq 1$ cm) were recorded across the FE, including the DDF and LMF, representing 212 species, 140 genera, and 67 families. Regarding trees with $\text{DBH} \geq 4.5$ cm (tree), 165 species, 116 genera, and 58 families were recorded. Regarding $\text{DBH} < 4.5$ cm (sapling), 189 species, 129 genera, and 63 families were recorded. The tree stem density was 1279 individuals/ha and the basal area was $30.48 \text{ m}^2/\text{ha}$. Sapling stem density was 3,051 individual/ha and the basal area was $0.59 \text{ m}^2/\text{ha}$ (Table 1). The dominant families based on species numbers were Rubiaceae, Phyllanthaceae, Fagaceae, Lauraceae, and Fabaceae, with 17, 15, 14, 13, and 11 species, respectively.

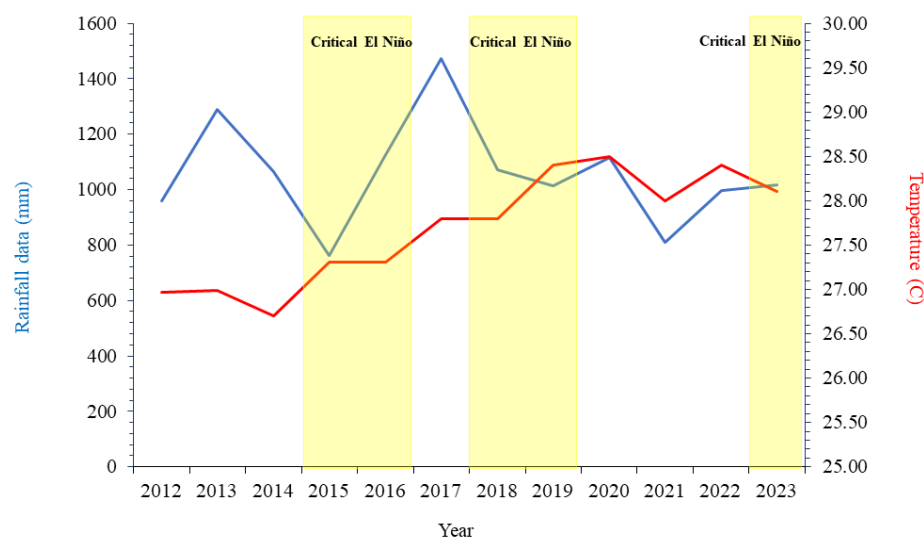


Figure 2. Climatic factors data: El Nino Southern Oscillation–Oceanic Nino index from 2012 to 2023 related to average rainfall (blue line) and temperature (red line) per year from Doi Suthep-Pui National Park Weather Station.

Table 1. Summary data of forest dynamics of trees (DBH ≥ 4.5 cm) in the forest ecotone permanent plot.

	2012	2014	2016	2018	2023	Average
Basal area (m ² /ha)	29.97	32.34	31.86	31.04	31.07	
Loss (m ² /ha)	0.54	1.51	0.47		1.84	1.09 $\pm$ 0.6
Gain (m ² /ha)	2.91	1.03	0.89		1.09	1.48 $\pm$ 0.9
Species number						
Sapling	142	165	175	189	192	172 $\pm$ 18
Tree	98	99	102	165	168	126 $\pm$ 33
Density (individual/ha)						
Saplings	2566	2851	3035	2816	3051	2864 $\pm$ 197
Trees	1263	1697	1673	1221	1279	1427 $\pm$ 237
Mortality rate (%/yr)						
Saplings	1.98	8.56	5.3	1.28		4.28 $\pm$ 3.35
Trees	1.4	3.56	4.26	1.94		2.81 $\pm$ 1.34
Recruitment rate (%/yr)						
Saplings	5.54	7.83	5.35	5.98		6.18 $\pm$ 1.13
Trees	0.51	1.0	0.98	0.83		0.83 $\pm$ 0.23

The forest dynamics of trees (DBH ≥ 4.5 cm) during 2012–2023 fluctuated during the monitoring period. The basal area tended to increase during the first period (2012–2014) from 29.97 m² to 32.34 m², contrasting with the second (2014–2016) and third (2016–2018) periods. In the last period, with a 5-year interval (2018–2023), the total basal area slightly increased by 0.03 m²/ha from 31.04 m²/ha (Table 1). A higher loss rate than gain rate was observed, particularly for increased mortality at the tree stage. However, size-dependent

mortality was significantly different among the periods, especially in the small size class (DBH < 4.5 cm) (Table 2). In addition, the average mortality rate in the sapling stage was higher than that in the tree stage overall (4.28 ± 3.35 and 2.81 ± 1.34 %/yr, respectively). However, the average recruitment rate at the sapling stage was approximately 7.5-fold higher than that at the tree stage, with rates of 6.18 ± 1.13 and 0.83 ± 0.23 %/yr, respectively. This indicates that mortality at the tree stage had a high impact on basal area changes; however, the high sapling stage recruitment supported high species numbers, with a total of 212 species recorded in 2023.

Table 2. Number of recruitment and dead trees of each period in the forest ecotone permanent plot.

Forest Dynamics Period	Number of New Trees			Number of Dead Trees		
	Overall	Trees	Saplings	Overall	Trees	Saplings
First (2012–2014)	626	24 ^c	602 ^b	264	65	199 ^c
Second (2014–2016)	951	50 ^b	901 ^b	1001	175	836 ^{ab}
Third (2016–2018)	1088	71 ^b	1017 ^b	1197	292	905 ^a
Fourth (2018–2023)	3574	156 ^a	3418 ^a	836	219	617 ^b
<i>p</i> -value		*	**		ns	*
CV (%)		4.6	5.4		16.18	5.8

Note: ns, *, **: Non-significantly different and significantly different at $p \leq 0.05$ and $p \leq 0.01$, respectively. Means within a column followed by the same letter are non-significantly different at $p \leq 0.05$ according to DMRT. CV (%) is the coefficient of variation.

GLM analysis, which detects the relationship between forest dynamics, mortality (number of dead trees), and recruitment (number of new trees), showed that only the mortality of trees and saplings was significantly correlated with decreasing rainfall and increasing temperatures (Table 3). In particular, the prolonged drought during the second monitoring period was negatively affected by the reduced rainfall ($p < 0.05$); the rain-free days were <52 (158 days in 2014 and 106 days in 2016) and positively correlated with increased temperature ($p < 0.01$) (Table 3). The patterns observed during the third and fourth census periods were similar to those observed during the first period. The mortality of saplings was particularly sensitive to the decreased rainfall and prolonged dry season. During the fourth census period, a significant increase in recruitment was observed, particularly in relation to the average rainfall for the tree and sapling stages.

Table 3. GLM analysis of the relationships between mortality (number of dead trees) and recruitment (number of new trees) (DBH ≥ 4.5 cm) and saplings (DBH < 4.5 cm) and environmental factors.

Forest Dynamics Period	First		Second		Third		Fourth	
	Rainfall	Temp.	Rainfall	Temp.	Rainfall	Temp.	Rainfall	Temp.
Trees								
Mortality (stem)	ns	ns	−1.05 *	+4.31 **	ns	ns	ns	ns
Recruitment (stem)	+1.45 *	ns	ns	ns	ns	ns	+1.35 *	ns
Saplings								
Mortality (stem)	ns	ns	−1.63 *	+3.53 **	−5.17 **	+1.71 *	ns	ns
Recruitment (stem)	+5.31 **	ns	ns	ns	ns	ns	+2.14 *	ns
Average	1103.6 mm/yr	26.9 °C	943.3 mm/yr	27.0 °C	1271.5 mm/yr	27.8 °C	990.8 mm/yr	28.28 °C

Note: Temp. = average temperature in each period; rainfall = average rainfall in each period. ns, *, **: non-significantly different and significantly different at $p \leq 0.05$ and $p < 0.01$, respectively.

The dynamics of tree-stage species (DBH ≥ 4.5 cm) in Thailand, based on the work of Marod et al. [43] and Nutiprapun et al. [19], reveal distinct patterns among evergreen and deciduous species. Dominant deciduous species included *Aporosa villosa* (Wall. ex

Lindl.) Baill., *Aporosa nigricans* Hook. f., *Dipterocarpus obtusifolius* Teijsm. ex Miq., *Quercus brandisiana* Kurz, *Rothmannia sootepensis* (Craib) Bremek., and *Wendlandia paniculata* (Roxb.) DC., while the dominant evergreen species included *Castanopsis tribuloides* (Sm.) A. DC., *Castanopsis acuminatissima* (Blume) A. DC., *Litsea martabarnica* (Kurz) Hook. f., *Tarennoidea wallichii* (Hook. f.) Tirveng. & Sastre, *Schima wallichii* (DC.) Korth., *Myrsine seguinii* H. Lév., and *Persea gamblei* (Hook. f.) Kosterm. The overall tree mortality and recruitment rates for the dominant deciduous species group in DDF were balanced during the first and second census periods (<10%/yr) (Figure 3A,B). In contrast, the dominant evergreen species group in the LMF exhibited significant fluctuations in overall mortality and recruitment rates. Mortality rates were significantly negatively correlated with decreased rainfall ($p < 0.05$), with a notable increase during the second period for *Castanopsis acuminatissima* (Blume) A. DC., *Castanopsis acuminatissima* (Blume) A. DC., *Litsea martabarnica* (Kurz) Hook. f., *Tarennoidea wallichii* (Hook. f.) Tirveng. & Sastre, *Schima wallichii* (DC.) Korth., *Myrsine seguinii* H. Lév., and *Persea gamblei* (Hook. f.) Kosterm. (Figure 3). During the third and fourth periods, the pioneer species of the LMF, specifically *Schima wallichii* (DC.) Korth. and *Myrsine seguinii* H. Lév., exhibited relatively similar recruitment and mortality rates (Figure 3C,D). These species can survive during periods of environmental change or suboptimal conditions, but eventually die if the conditions remain unsuitable. For the dominant tree species in the LMF, particularly those from the Fagaceae family, recruitment rates were lower than mortality rates during both periods. In contrast, pioneer tree species in deciduous forests, such as *Rothmannia sootepensis* (Craib) Bremek., *Aporosa villosa* (Wall. ex Lindl.) Baill., and *Aporosa nigricans* Hook. f., showed higher growth rates than mortality rates. *Dipterocarpus obtusifolius* Teijsm. ex Miq. and *Quercus brandisiana* Kurz (Figure 3C,D), dominant in deciduous forests, had similar recruitment and mortality rates throughout the study period. This suggests that drought conditions have a strong impact on the mortality of evergreen species and may have led to an increase in the prevalence of drought-resistant deciduous species in FEs.

The overall RGR for the entire community was 1.54 ± 0.42 cm/yr. Among the four repeated measurement periods, the fourth period (2018–2023) had the highest growth rate at 2.16 cm/yr, followed by the second period (2014–2016) at 1.43 cm/yr, third period (2016–2018) at 1.34 cm/yr, and first period (2012–2014) at 1.22 cm/yr. Among the 20 most abundant and widely distributed species in the permanent plot, which comprised approximately 60% of the individuals (Table 4), there was significant variation in RGR. The evergreen species had a slightly higher average annual RGR (1.54 ± 0.29 cm/yr) than the deciduous species (1.50 ± 0.26 cm/yr). Among the 40 species analyzed, *Lithocarpus truncatus* (King ex Hook. f.) Rehder exhibited the highest growth rate (2.25 ± 0.59 cm/yr), while *Memecylon plebejum* Kurz var. *ellipsoideum* Craib had the lowest at 1.08 ± 0.31 cm/yr (Table 4).

Regarding the saplings stage, $1 \text{ cm} \leq \text{DBH} < 4.5 \text{ cm}$, the result in 2023 showed that there were 9153 individuals, with a density of 3051 individuals/ha across the permanent plot, with 175 species belonging to 118 genera, and 59 families. The dominant families based on species number were Rubiaceae, Fagaceae, and Lauraceae, with 14, 13, and 12 species, respectively. Sapling dynamics exhibited trends similar to those observed during the three stages. Our analysis of the period between 2012 and 2023 revealed that the overall average recruitment rate ($6.18 \pm 1.13\%$ /yr) was higher than the overall average mortality rate ($4.28 \pm 3.35\%$ /yr) and varied among different periods. Notably, the mortality rate increased nearly seven-fold during the second period (2014–2016); however, the recruitment rates remained relatively constant, ranging from 5 to 7% per year throughout the survey period (Table 2). Among the dominant species, evergreen pioneer species, such as *Tarennoidea wallichii* (Hook. f.) Tirveng. & Sastre, *Myrsine seguinii* H. Lév., and *Litsea martabarnica* (Kurz)

Hook. f., had higher recruitment rates than mortality rates. Contrasting patterns were observed in deciduous species, including *Irvingia malayana* Oliv. ex A. W. Benn., *Aporosa villosa* (Wall. ex Lindl.) Baill., and *Vitex peduncularis* Wall. ex Schauer. These species had low recruitment rates; however, mortality rates were absent during some of the monitored periods. This suggests that these deciduous species may have been more resistant to the environmental changes in the study area (Figure 4).

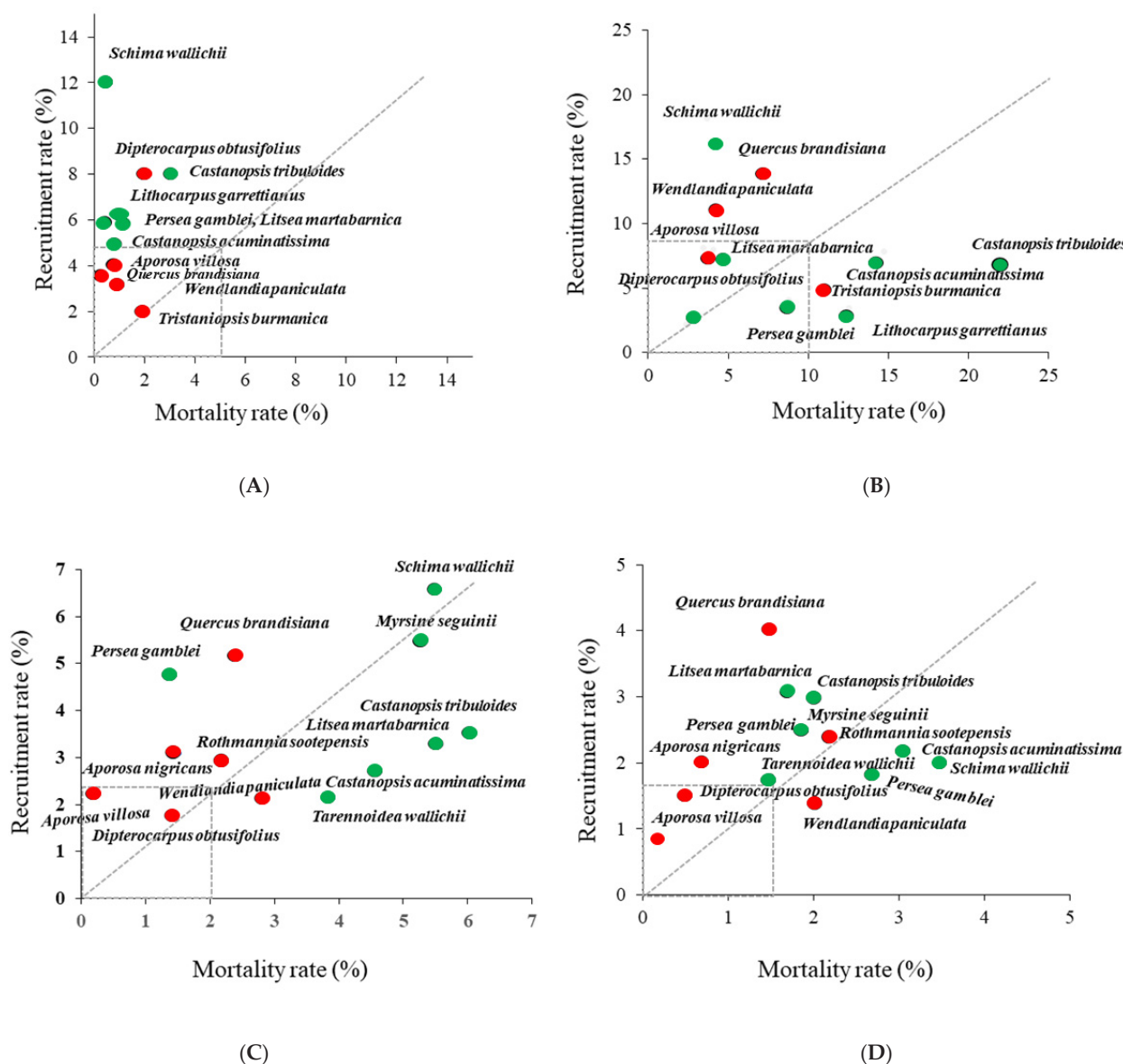


Figure 3. Relationship between recruitment and mortality rates of dominant tree species during each forest dynamics census period: (A) first period (2012–2014), (B) second period (2014–2016), (C) third period (2016–2018), and (D) fourth period (2018–2023); red points are deciduous species and green points are evergreen species.

Table 4. Tree species dynamics of relative growth rate (RGR) 11 years (2012–2023) in the forest ecotone permanent plot.

Species Name	Ecological Niche	No. Tree	Period 1	Period 2	Period 3	Period 4	Average $\pm$ SD
<i>Anneslea fragrans</i> Wall.	evergreen	30	1.42	1.42	1.45	2.30	1.65 $\pm$ 0.44
<i>Antidesma sootepense</i> Craib	deciduous	8	1.09	1.12	1.65	2.31	1.55 $\pm$ 0.57
<i>Aporosa nigricans</i> Hook. f.	deciduous	66	1.06	1.04	1.07	1.74	1.23 $\pm$ 0.34
<i>Aporosa villosa</i> (Wall. ex Lindl.) Baill.	deciduous	69	1.05	1.04	1.08	1.73	1.23 $\pm$ 0.34
<i>Archidendron clypearia</i> (Jack) I. C. Nielsen	deciduous	11	1.21	1.16	1.24	1.98	1.40 $\pm$ 0.39
<i>Canarium subulatum</i> Guillaumin	deciduous	14	1.49	1.49	1.48	2.45	1.73 $\pm$ 0.48
<i>Castanopsis armata</i> (Roxb.) Spach	evergreen	16	1.36	1.41	1.51	2.41	1.67 $\pm$ 0.50
<i>Castanopsis tribuloides</i> (Sm.) A. DC.	evergreen	46	1.49	1.53	1.62	2.50	1.78 $\pm$ 0.48
<i>Cinnamomum iners</i> Reinw. ex Blume	evergreen	25	0.84	1.29	1.08	1.79	1.25 $\pm$ 0.40
<i>Cratoxylum formosum</i> (Jacq.) Benth. & Hook. f.	deciduous	38	1.00	1.09	1.14	1.84	1.27 $\pm$ 0.39
<i>Diospyros vera</i> (Lour.) A. Chev.	evergreen	30	1.18	1.22	1.18	1.88	1.36 $\pm$ 0.34
<i>Dipterocarpus obtusifolius</i> Teijsm. ex Miq.	deciduous	112	1.62	1.65	1.69	2.73	1.92 $\pm$ 0.54
<i>Dipterocarpus tuberculatus</i> Roxb.	deciduous	60	1.50	1.48	1.50	2.40	1.72 $\pm$ 0.45
<i>Eriobotrya bengalensis</i> (Roxb.) Hook. f.	evergreen	104	1.13	1.10	1.10	1.82	1.29 $\pm$ 0.36
<i>Eurya acuminata</i> (Roxb.) Hook. f.	evergreen	2	1.35	1.45	1.51	2.32	1.66 $\pm$ 0.45
<i>Gardenia sootepensis</i> Hutch.	deciduous	7	1.00	0.96	0.97	1.64	1.14 $\pm$ 0.33
<i>Helicia nilagirica</i> Bedd.	evergreen	12	1.12	1.10	1.09	1.76	1.26 $\pm$ 0.33
<i>Irvingia malayana</i> Oliv. ex A. W. Benn.	deciduous	12	1.73	1.71	1.65	2.77	1.96 $\pm$ 0.54
<i>Lithocarpus truncatus</i> (King ex Hook. f.) Rehder	evergreen	4	1.97	1.93	1.95	3.13	2.25 $\pm$ 0.59
<i>Litsea martabarnica</i> (Kurz) Hook. f.	evergreen	350	1.05	1.04	1.05	1.71	1.21 $\pm$ 0.33
<i>Magnolia baillonii</i> Pierre	evergreen	35	1.36	1.63	1.50	2.38	1.72 $\pm$ 0.45
<i>Melientha suavis</i> Pierre	deciduous	5	0.84	1.35	1.09	1.79	1.27 $\pm$ 0.41
<i>Memecylon plebejum</i> Kurz var. <i>ellipsoideum</i> Craib	evergreen	16	0.92	0.88	0.97	1.54	1.08 $\pm$ 0.31
<i>Myrsine seguinii</i> H. Lév.	evergreen	219	1.13	1.26	1.19	1.99	1.39 $\pm$ 0.40
<i>Persea gamblei</i> (Hook. f.) Kosterm.	evergreen	57	1.21	1.33	1.29	2.07	1.47 $\pm$ 0.40
<i>Phoebe lanceolata</i> (Nees) Nees	evergreen	44	1.05	1.05	1.07	1.80	1.24 $\pm$ 0.37
<i>Prunus arborea</i> (Blume) Kalkman	evergreen	2	1.70	1.70	1.76	2.77	1.99 $\pm$ 0.53
<i>Quercus brandisiana</i> Kurz	deciduous	318	1.47	1.48	1.52	2.43	1.73 $\pm$ 0.47
<i>Quercus kerrii</i> Craib	deciduous	23	1.53	1.52	1.52	2.40	1.74 $\pm$ 0.44
<i>Quercus oidocarpa</i> Korth.	evergreen	15	1.32	1.42	1.40	2.28	1.61 $\pm$ 0.45
<i>Rothmannia sootepensis</i> (Craib) Bremek.	deciduous	106	1.11	1.09	1.12	1.77	1.27 $\pm$ 0.33
<i>Schima wallichii</i> (DC.) Korth.	evergreen	156	1.60	1.59	1.60	2.58	1.84 $\pm$ 0.49
<i>Semecarpus cochinchinensis</i> Engl.	deciduous	29	1.29	1.29	1.29	2.06	1.48 $\pm$ 0.39
<i>Shorea obtusa</i> Wall. ex Blume	deciduous	37	1.37	1.41	1.39	2.30	1.62 $\pm$ 0.46
<i>Syzygium albiflorum</i> (Duthie ex Kurz) Bahadur & R. C. Gaur	evergreen	30	1.36	1.63	1.50	2.41	1.73 $\pm$ 0.47
<i>Syzygium claviflorum</i> (Roxb.) Wall. ex A. M. Cowan & Cowan	evergreen	44	1.47	1.58	1.50	2.30	1.71 $\pm$ 0.40
<i>Tarennoidea wallichii</i> (Hook. f.) Tirveng. & Sastre	evergreen	110	1.27	1.30	1.29	2.08	1.49 $\pm$ 0.40
<i>Tristaniaopsis burmanica</i> (Griff.) Peter G. Wilson & J. T. Waterh.	deciduous	25	1.21	1.36	1.32	2.15	1.51 $\pm$ 0.43
<i>Turpinia cochinchinensis</i> (Lour.) Merr.	evergreen	50	1.03	1.07	1.05	1.72	1.22 $\pm$ 0.34
<i>Wendlandia paniculata</i> (Roxb.) DC.	deciduous	283	1.06	1.06	1.11	1.75	1.25 $\pm$ 0.33

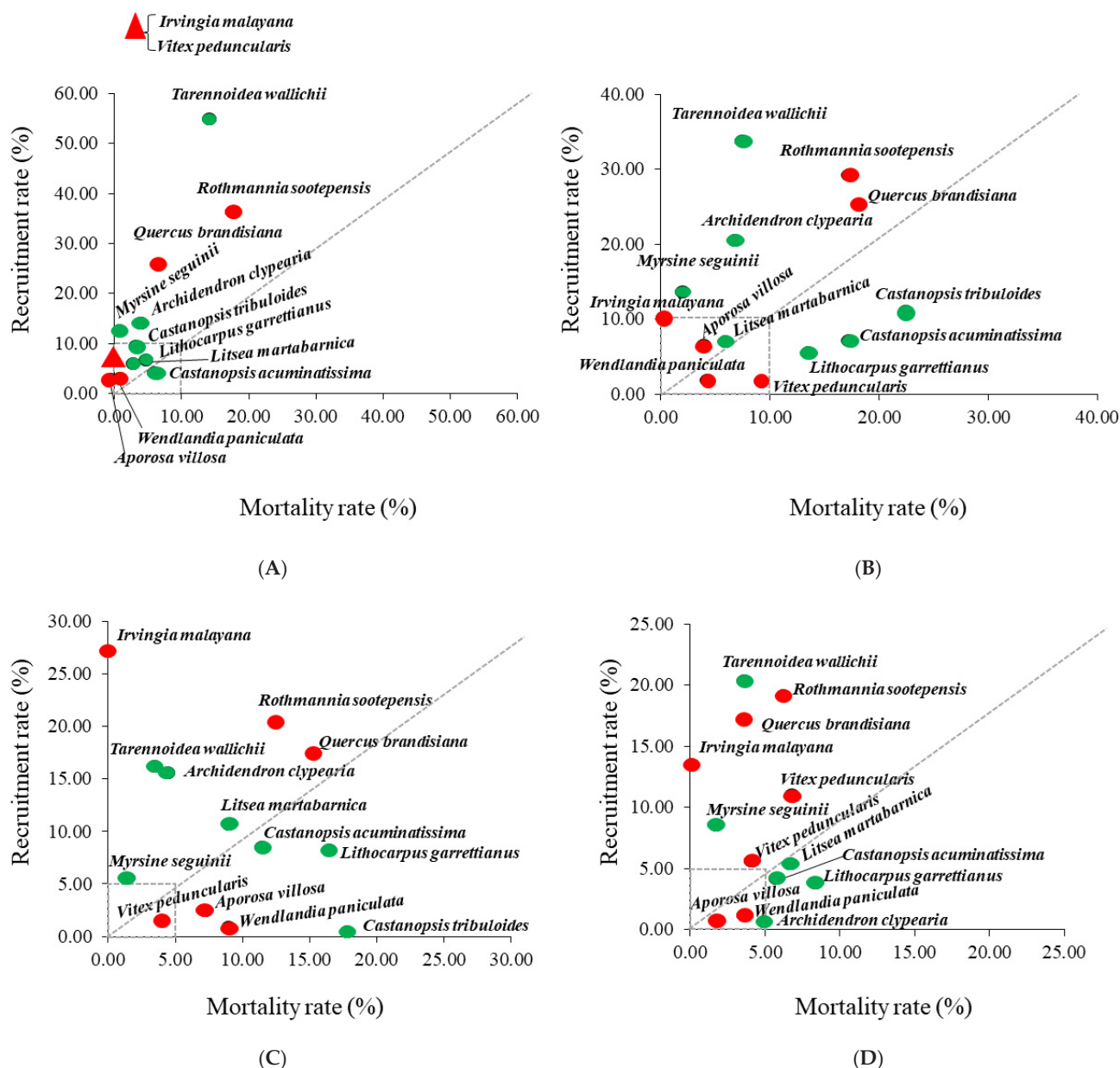


Figure 4. Relationship between the recruitment and mortality rates of dominant sapling species during each forest dynamics census period: (A) first period (2012–2014), (B) second period (2014–2016), (C) third period (2016–2018), and (D) fourth period (2018–2023); red points are deciduous species and green points are evergreen species.

4. Discussion

The species predominantly found in FEs in the LMF, such as *Litsea martabarnica* (Kurz) Hook. f., *Myrsine seguinii* H. Lévl., and *Wendlandia paniculata* (Roxb.) DC. [32], exhibited a constant recruitment rate. However, the dominant species in the LMF showed high mortality rates at the sapling and tree stages during each monitoring period. Mortality rates varied among the species and were strongly influenced by environmental changes, with severe drought conditions affecting evergreen species. Conversely, increased rainfall may enhance the recruitment rate and induce the coexistence of a large number of species at the FE. This finding supports the successful establishment of coexisting sapling species in these areas. Similar findings were also observed among mature tree species in the DDF and LMF [19,32,43]. However, some reports have shown that some dominant evergreen species, such as *Castanopsis tribuloides* and *Castanopsis acuminatissima*, can be found in forest

gaps and at the edges of the LMF [44,45], although these species appear to be less adapted to drought conditions in the study area. By categorizing species based on mortality and recruitment rates, we can identify distinct ecological strategies that reflect either resilience or vulnerability to disturbances, such as increasing of stem density, which would likely lead to competition and have a negative impact on growth and survival. For example, the dominant deciduous species had higher recruitment rates than mortality rates, indicating effective regeneration and favorable growth conditions. Their stable mortality–recruitment relationship implies their successful adaptation to environmental factors, especially in FEs zone.

The RGRs of tree species in permanent plots did not vary significantly among different ecological niche types based on leaf habits (evergreen and deciduous species). This lack of difference may be attributed to the adequate environmental conditions available in these plots, particularly those located in forest ecotone zones between deciduous and evergreen forests within the mountain ecosystem. The pioneer and climax species groups showed similar growth rates, likely because of the dense co-existence of trees in these areas [43,46]. According to Lin et al. [47] and Arriaga-Ramírez et al. [48], the growth rates of trees in tropical rainforests typically range from 1.5 to 2 cm per year, and are often inversely related to the availability of limited resources at different temporal and spatial scales. This variability in growth rates and responses is also influenced by regeneration strategies, maximum size, and species associations with specific edaphic and climatic conditions [49].

The forest dynamics of the study area revealed significant variations across different species and periods that were closely linked to environmental changes, particularly climate events such as drought and El Niño. These factors exerted a substantial influence on forest structure and species composition. Climatic conditions are critical environmental factors for plant regeneration, especially during the sapling stage, and plants are highly sensitive to such changes [11,33]. This study further elucidates that variations in rainfall and temperature are key determinants of sapling survival in both the LMF and DDF along altitudinal gradients, which is consistent with the findings of Laurance et al. [5] and Martin et al. [50]. Deciduous species, which are well adapted to drought conditions, often show high recruitment rates at both the sapling and tree stages and can thrive at higher altitudes. In contrast, evergreen species, which are more susceptible to microclimate changes, tend to have higher mortality rates. The spatial distribution of species is also influenced by other environmental factors, such as topographic elevation, which plays a substantial role in tree distribution [16,18]. In particular, evergreen tree species (Fagaceae and Lauraceae) are often associated with higher elevations and lower temperatures [51,52]. The dominant tree species in the FE between the DDF and LMF can be categorized into three groups based on altitude: low, intermediate, and high land species. Additionally, soil texture, which ranges from sandy to sandy clay loam, significantly affects tree distribution (deciduous tree species) [53,54]. Generalist species, often characterized as pioneer species, are highly distributed in ecotone areas (elevation 940–980 m a.s.l.). Thus, spatial distribution is influenced by ecological niche, especially in environmental gradients [55]. Understanding the responses (sensitive or strong) of plant species to environmental changes and understanding their niches can be important in plant conservation and restoration programs in mountain ecosystems.

5. Conclusions

Long-term studies of forest ecology provide valuable indicators of how tree dynamics respond to changes in environmental factors such as increasing light intensity, drought conditions, and temperature changes. These changes can affect tree regeneration differently depending on the species and ecological niche. Environmental changes have a significant

effect on species coexistence, particularly in FEs between the DDF and LMF, where intermediate environmental conditions are observed. High mortality rates were predominantly observed in the dominant evergreen species of the LMF, which were positively correlated with decreased rainfall and increased temperatures. This suggests that drought conditions strongly influence tree mortality, particularly in evergreen species. In contrast, deciduous species in the DDF increased in density, particularly in the FE, indicating their higher adaptability to drought conditions. This adaptability may allow them to occupy FEs more effectively than the LMF species.

Thus, understanding coexisting species and their ecological niches along altitudinal gradients is crucial for effective restoration programs, particularly in mountain ecosystems. Tree species should be categorized based on their preferences regarding drought resistance, moisture conditions, light requirements, and other factors. By selecting species that are well-suited to the specific environmental conditions of the restoration areas, this approach can create optimal conditions for successful species establishment. Consequently, this tailored approach can accelerate the recovery of forests to their climactic state and achieve restoration goals within a short time frame.

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