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Seedling Recruitment at the Upper Limit of Tree Growth in the Alborz Mountains, Northern Iran: Safe Site Characteristics and Edaphic Conditions

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Abstract: Climate warming may enhance the upslope migration of tree species at high elevations. In this context, few studies have analyzed the requirements of tree seedlings with respect to safe sites and soil conditions, particularly in the Alborz Mountains (Iran). We collected regeneration and environmental data focusing on small seedlings and young saplings at the upper limit of tree growth in the Alborz Mountains. For each life stage, we assessed the association of seedlings with safe site conditions (rocks, stones, deadwood, and canopy shade), microhabitat substrates (vegetation, litter, bare soil, and stones), and soil variables along elevational gradients. Our findings revealed strong associations between seedlings and facilitative elements (tree shade, deadwood, rocks, and stones). Fewer associations were observed with microhabitat substrates. These associations differed between the two establishment stages. In addition, seedlings of both life stages exhibited distinct associations with soil variables (total nitrogen, sand, and bulk density). The contrasting relationships between small seedlings and young saplings with safe site conditions, microhabitat substrates, and soil variables suggest that early life stages may have different site requirements compared to later stages. Our results suggest that the potential for upslope migration of tree species may depend on safe site conditions, particularly those provided by tree shade, deadwood, rocks, and stones.

Keywords: elevational gradient; Hyrcanian forests; Iran; microhabitats; saplings; seedling recruitment; soil conditions

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1. Introduction

It is likely that climate change will cause trees at high elevations to move upslope, as plant life at high elevations is largely controlled by abiotic factors such as low temperatures and other harsh climatic conditions [1–3]. An essential prerequisite for this movement is successful seedling establishment and low mortality in pre-established life stages at elevations above the uppermost tree individuals [4]. However, establishment and mortality rates can vary between different seedling/sapling life stages and among different tree species [5,6]. Thus, information on the required safe sites and microhabitat conditions is needed. Such information facilitates the assessment of the effects of climate warming on the potential upslope migration of tree species and the prediction of future tree advancement in terms of successful recruitment and mortality in the treeline ecotone [7–12].

Seedlings may be more dependent on shelter elements (e.g., topographic shelters, rocks, and stones) or microhabitats [5,13] as a result of harsher environments when migrating to higher elevations where safe sites are probably even more important for a successful regeneration [14].

Safe sites for successful tree regeneration have not been characterized to date in the Alborz Mountains. This mountain range is located in northern Iran, along the southern coast of the Caspian Sea, and ranges in elevation from 26 m below sea level to the peak of Mount Damavand, which rises to 5671 m above sea level. The northern slopes receive significant rainfall, creating a temperate climate that supports the growth of Hyrcanian forests, a type of temperate deciduous forest [15–17]. The upper limit of these forests varies between 2400 and 2850 m above sea level [18–20].

Seedling establishment in relation to safe site conditions in the Hyrcanian forests has not yet been the subject of analysis. Since seedling establishment is a crucial factor for the spatial pattern in treeline ecotones and for the upslope migration of tree species, the respective regeneration studies could contribute to the explanation of the gap between the current and potential upper limit of trees in the Alborz Mountains. To the best of our knowledge, most studies on the Hyrcanian forests are mainly related to mature trees e.g., [18,20], while seedlings and saplings have been poorly assessed. For example, Naqinezhad et al. [21] assessed the importance of soil variables on understorey growth forms in the Hyrcanian forests, while seedlings and saplings were not among the investigated groups.

In order to elucidate the role of seedling establishment at the upper limit of tree growth on the northern slopes of the Alborz Mountains, we evaluated the dependence of seedling establishment on site conditions and its relationship with soil variables, addressing the following research questions: 1—Which facilitative elements and microhabitat substrates provide safe sites for the successful establishment of tree seedlings? 2—How does the dependence of seedlings on facilitative elements and microhabitat substrates vary between different life stages (small seedlings vs. young saplings)? 3—How do soil variables influence the successful recruitment of tree species, and do these relationships vary between different life stages?

2. Materials and Methods

2.1. Study Area

The Hyrcanian forests are one of the rare temperate deciduous forest zones in the predominantly arid and semi-arid landscapes of the Middle East. Designated as a UNESCO World Heritage Site in 2019, these forests extend along the northern slopes of the Alborz Mountains (northern Iran) over ca. 800 km up to Azerbaijan on the southern/southwestern shores of the Caspian Sea [15]. The flora and vegetation of the Hyrcanian forests are characterized by Euro-Siberian floristic elements, with Irano-Turanian elements dominating in the upper altitudinal zones [15–19,22]. At the same time, the Hyrcanian ecoregion is a part of the Caucasus biodiversity hotspot and a refuge for the Arcto-Tertiary relict flora [23–25].

A humid temperate–subtropical climate with high amounts of precipitation (between 500 and 1500 mm per year) allows for the development of broadleaf forest communities in the Hyrcanian forests. Records from the climate station nearest to the study area, Nowshahr, show an average annual precipitation of 1300 mm and an average annual temperature of 16.5 °C at the Caspian Sea coast. However, at elevations > 1500 m, most of the annual precipitation falls as snow in late autumn, winter, and early spring [19].

Gholizadeh et al. [26] provided a detailed classification of the vegetation of the Hyrcanian forests along altitudinal and longitudinal gradients in northern Iran. Their study showed that altitude and mean annual temperature were the most important environmental variables influencing the composition and distribution of vegetation types in these forests. In addition to topo-climatic factors, soil variables also play a critical role in shaping species composition. The plant communities and associations identified in these forests are distributed altitudinally into lowland forests, submontane, montane, and upper-montane forests. The upper-montane forests are mainly dominated by *Fagus orientalis* (up to 2700 m a.s.l.) and, at higher altitudes, by *Quercus macranthera*. At these altitudes, the *Fagus orientalis* forest reaches its highest point (2700 m a.s.l.). It contains many shrubs and herbs from ecotones, such as *Sorbus aucuparia* and *Viburnum lantana*. *Quercus macranthera* and *Acer hyrcanum* are common on rocky slopes in the upper montane belt between 2200 and 2700 m a.s.l. *Carpinus orientalis* can grow at even higher elevations, where it becomes shrubland [26]. These upper limits are far below the climatic treeline, i.e., the elevational zones above the uppermost *Quercus macranthera* occurrences are bioclimatically suitable for tree growth up to about 3300 m, but trees are absent [19]. The causes of this gap between the current and potential upper limit of trees have not yet been sufficiently analyzed. Millennia of land use in the Alborz have been suggested as a major driver [19].

2.2. Data Sampling

We collected seedling data along three elevational transects ranging from a closed forest to the uppermost limit of tree growth on the ridge of Shah-Alamdar Peak (2390–2640 m a.s.l.) in July 2022, Tabar-Kuh Peak (2431–2714 m a.s.l.) in July 2023, and Kuhe-Golijan Peak (2286–2778 m a.s.l.) in June 2023. We divided each transect into three zones: closed forest (zone A), the uppermost closed forest (zone B), and the upper limit of tree growth (zone C) (Figure 1). We surveyed three randomly selected 20 × 20 m plots, except at Tabar-Kuh, where two plots were surveyed due to the topographic constraints of a narrow valley. To avoid proximity between plots and the valley edge, we spaced them accordingly. Additionally, we included data from three more plots in zone C (at Gazna-No, near the peak of Korma-Kuh), where we recorded the highest elevation of tree growth in the region at 2960 m. In total, we established 27 vegetation plots.

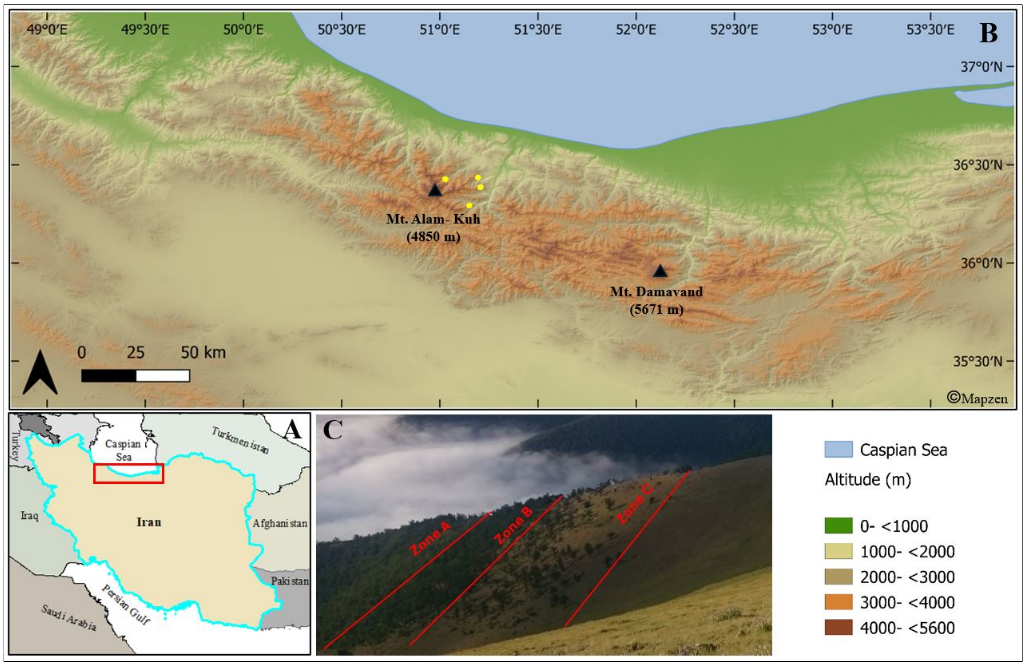

Figure 1. The study area. (**A**): Iran and surrounding countries in the Middle East; the Alborz Mountains in northern Iran are highlighted (red rectangle). (**B**): Central and western parts of the Alborz Mountains, with yellow indicating the study sites. (**C**): Zones A, B, and C at site SA (at the Shah-Alamdar ridge).

In each plot, seedlings and young saplings were identified to the species level, and the number of seedlings of each tree species was counted. To analyze the establishment stage of the seedlings, we measured their height from the ground to the shoot tip and counted the number of bud scars. The seedlings were categorized into two establishment classes. Class I (0–<10 cm) represents one-year-old seedlings, with over 87% of seedlings having a bud scar at or below 10 cm. Seedlings in the size range of 10–<50 cm was classified as young saplings in Class II. Further analyses were performed on these two classes by calculating the density of seedlings and saplings per hectare (ha) for each tree species.

To analyze microhabitat characteristics for seedling classes, we followed the method of Bürzle et al. [5]. Microhabitat information was recorded in circular sample plots around each individual seedling with plot diameters varying according to seedling height (seedling height: diameter of microsite; 0 to <10 cm: 10 cm diameter; 10 to <20 cm: 20 cm diameter;

20 to <30 cm: 30 cm diameter; 30 to <40 cm: 40 cm diameter; 40 to 50 cm: 50 cm diameter). We assessed the vegetation and substrate cover within each microhabitat, including the percentage of cover by vegetation, litter, bare soil, and stones. Additionally, we sampled facilitative elements within a 2 m radius of each seedling, recording the distance as the maximum distance to at least one potentially protective element for seedling growth [5]. We distinguished four types of facilitative elements: rocks (<60 cm diameter), stones (20–60 cm diameter), deadwood, and canopy shade. We also recorded the absence of these elements.

To predict the effect of soil variables on seedling density, we collected a soil sample from a depth of 0–10 cm at the center of each plot. An additional sample was taken to calculate bulk density using the clod method [27]. Soil texture was determined using the Bouyoucos hydrometer method [28]. Based on these results, soil types were determined based on soil texture triangle [29]. Organic carbon was estimated using the Walkley and Black method [30]. Soil total nitrogen content was analyzed by the semi-micro Kjeldahl method [31]. Soil pH was measured in a soil suspension with a ratio of 1:2.5 using a pH meter, and electrical conductivity (EC) was measured using an EC meter in a saturation extract. Available phosphorus (P) was measured spectrophotometrically using the Olsen method [32]. Atomic absorption spectrophotometry was employed to determine available potassium (K), calcium (Ca), and magnesium (Mg) according to the method of Bower et al. [33].

2.3. Data Analysis

The number of facilitative element observations, microhabitat substrate cover values, and seedling densities per class and zone were checked for normality and homogeneity of variance by visually inspecting the distribution of residuals [34]. We used generalized linear models (GLMs) [35,36] to assess the influence of facilitative elements, microhabitat substrates, and soil predictors on seedling density for the two classes per zone. Based on the distribution of the response variables, a binomial distribution GLM was applied using the '*MASS*' package ver. 7.3–58.1 [37] to test the importance of facilitative elements and microhabitat substrates. A negative binomial GLM with a log link was performed using the '*stats*' package ver. 4.2.2 to assess the effect of soil variables on seedling density.

Before conducting the statistical analyses, we checked all potential predictors within the soil variable sets for collinearity and differences between zones. We found that soil factors were similar between zones (Table 1) and did not show significant differences (Figure 2), whereas seedling density differed significantly between zones (Figure 3). Consequently, we focused the analyses on total nitrogen as a proxy for nutrients, sand as a texture element, and bulk density as a proxy for soil moisture and compaction to evaluate how well soil variables could predict seedling density per zone.

Table 1. Summary of environmental variables collected on the plots in each zone. The table provides an overview of key environmental variables measured across the different zones (A, B, and C), including soil and topographic properties. The soil type is defined on the basis of the most dominant soil types among the plots.

Environmental Variables	**Mean (Min–Max)**		
	Zone A (n = 8)	**Zone B (n = 8)**	**Zone C (n = 11)**
Elevation (m a.s.l.)	2384.6 (2286–2469)	2497.8 (2413–2554)	2697.4 (2574–2960)
Slope (%)	57.75 (45–69)	60.13 (50–68)	45.55 (10–71)
Sand (%)	58.5 (20–74)	53 (26–76)	59.45 (36–86)
Silt (%)	28.25 (16–60)	31.25 (14–56)	33.27 (10–50)
Clay (%)	13.25 (4–20)	13.5 (6–26)	8.55 (2–26)
Soil type	Sandy–loam	Sandy–loam	Sandy–loam
Bulk density (g cm^{-3})	1.25 (0.84–1.55)	1.58 (1.2–2.12)	1.72 (1.08–3.34)

Table 1. *Cont.*

Environmental Variables	Mean (Min–Max)		
	Zone A (n = 8)	**Zone B (n = 8)**	**Zone C (n = 11)**
CEC (ppm)	29.2 (28.12–30.2	29.37 (27.53–30.8)	29.52 (27.89–31.15)
pH (1:2.5 H_2O)	6.75 (5.2–7.35)	6.64 (5.9–7.41)	6.95 (6.13–7.72)
Electrical conductivity (EC) (ds m^{-1})	175.25 (46.6–317)	127.75 (58.5–253)	146.84 (60–310)
Organic C (%)	2.63 (1.62–3.86)	2.32 (1.2–2.7)	2.36 (1.68–2.7)
Total N (%)	0.16 (0.13–0.21)	0.15 (0.11–0.18)	0.15 (0.12–0.19)
C/N (%)	16.74 (12.46–19.29)	15.65 (10.91–17.73)	16.15 (12.92–19.14)
Available phosphorous (mg/kg)	14.25 (11–19)	12.5 (9–15)	11.27 (8–18)
Available potassium (mg/kg)	307.16 (129–556)	215.41 (124.25–390.5)	274.18 (101.75–536.25)
Available calcium (mg/kg)	570.56 (245.2–887.7)	412.94 (196.3–614.8)	504.65 (242.6–694.8)
Available magnesium (mg/kg)	268.74 (99.52–369.52)	204.66 (67.88–331.85)	119.68 (49.47–210.47)

The other soil types found in the plots are loam and silt–loam in zone A; loam, clay–loam, sand–clay–loam, and silt–loam in zone B; and loam, loam–sand, and sand–loam in zone C.

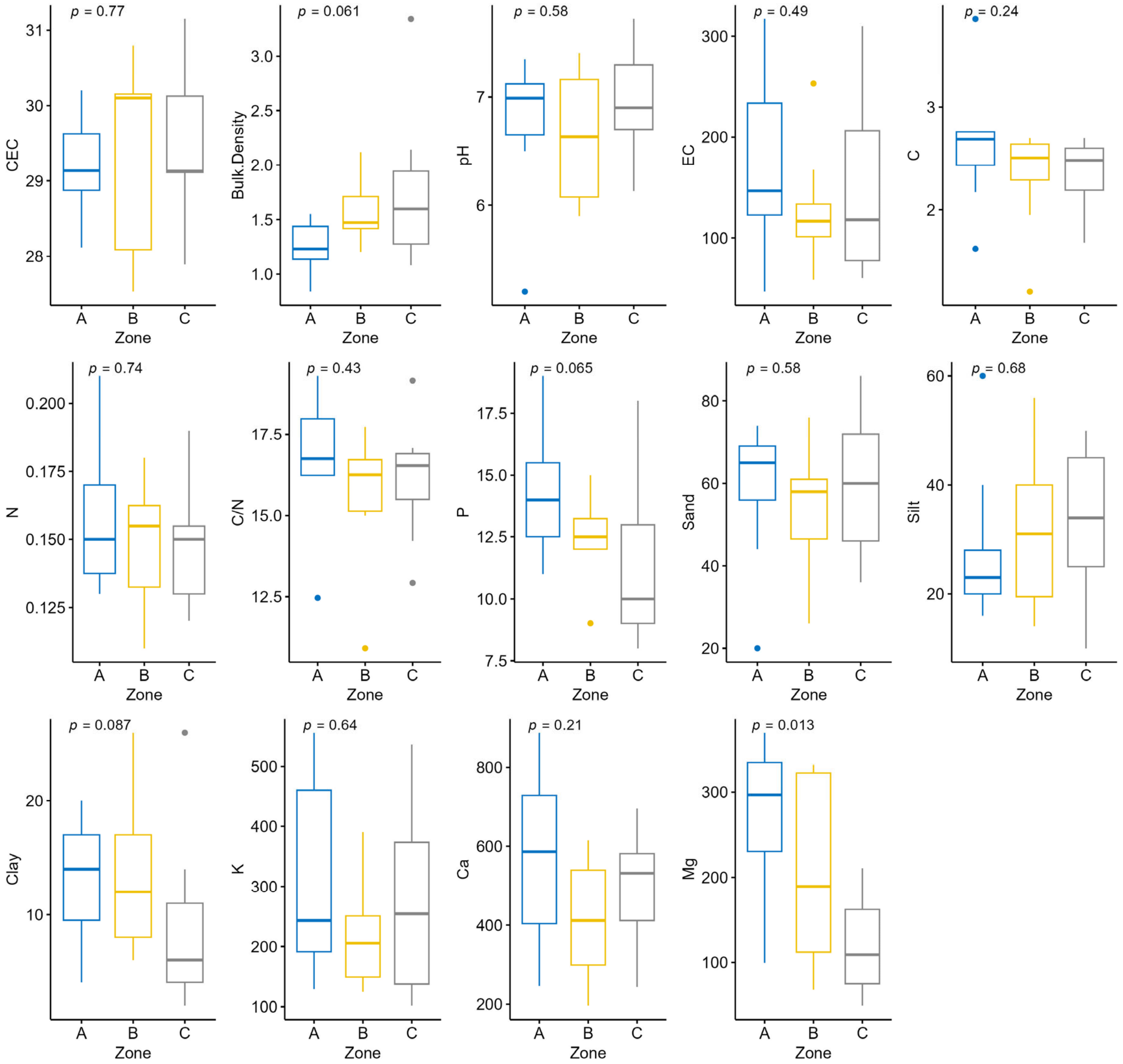

Figure 2. Differences in soil variables between zones using the Kruskal–Wallis test in the study area. Soil variables did not differ significantly between zones, except for available magnesium (Mg), which was highest in zone A (at lowest elevations) and lowest in zone C (at highest elevation).

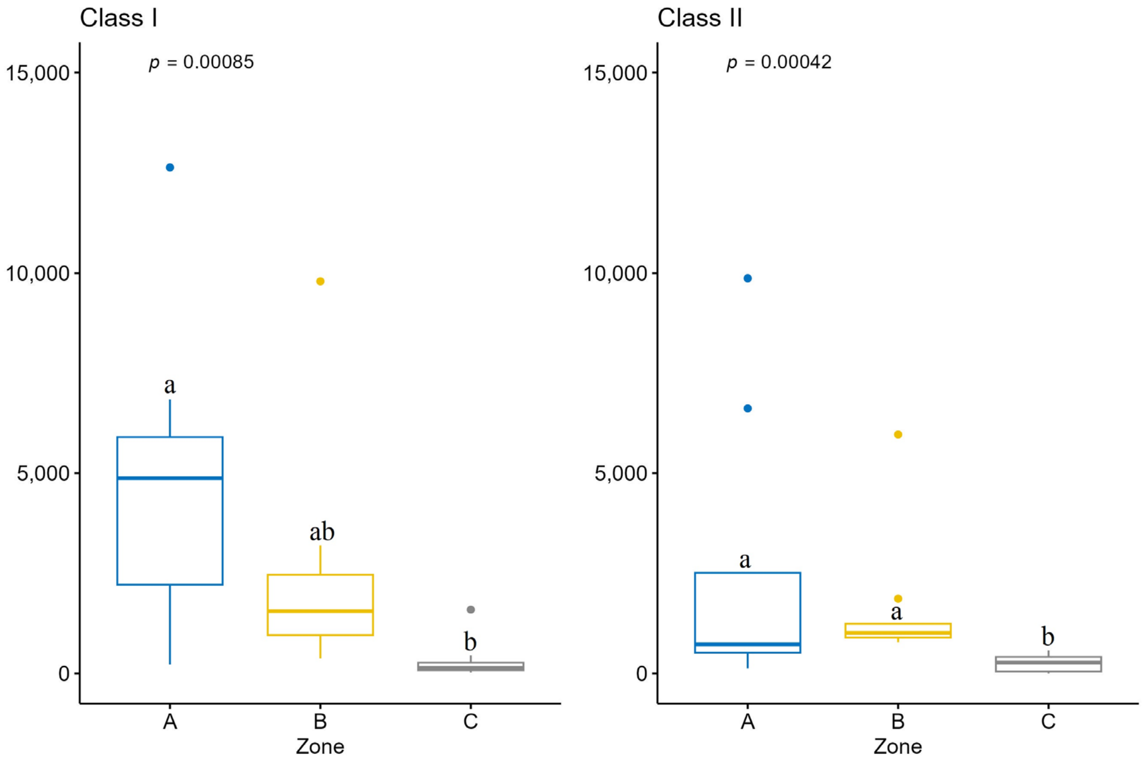

Figure 3. Seedling densities (N/ha) of Class I (0–<10 cm) and Class II (10–<50 cm) across different zones. Significant differences (p < 0.05) between zones were tested using the Kruskal–Wallis test. Different small letters indicate statistically significant differences between groups.

Figures were generated using the '*tidyverse*' ver. 2.0.0 [38], '*viridis*' 0.6.2 [39], and '*ggplot2*' ver. 3.4.4 [40] packages. All analyses were conducted in the R 4.2.2 statistical software environment [41].

3. Results

3.1. Distribution of Seedlings Along the Elevational Gradient

We counted a total of 5197 seedling individuals (sum of all species in all 27 plots across all zones), averaging 2435.65 per hectare in the study area. We observed a species- and zone-specific distribution: the total number of seedlings of all species per hectare for Class I (0–<10 cm) averaged 6621.88 in zone A, 2562.50 in zone B, and 1975 in zone C. For Class II (10–<50 cm), the averages were 2525 in zone A, 1675 in zone B, and 247.73 in zone C (see Figure 3 for species-specific seedling numbers).

As expected, the number of seedlings in Class I was higher than in Class II in all zones (Figure 4). In zone A, we recorded seedlings of 14 tree species, increasing to 19 species in zone B and decreasing to 10 species in zone C. In zone A, *Acer hyrcanum* and *Fagus orientalis* had the highest number of seedlings across all zones (Figure 3). However, in zone B, the number of Class II seedlings was higher for *Fagus orientalis* compared to *Acer hyrcanum*. In zone C, seedlings of *Fagus orientalis* were no longer present, while *Quercus macranthera* and *Carpinus orientalis* became more frequent, with *Acer hyrcanum* having the highest number of seedlings in this zone. Seedlings of *Acer hyrcanum*, *Quercus macranthera*, *Fraxinus excelsior*, *Sorbus torminalis*, *Acer monspessulanum*, *Acer platanoides*, *Prunus divaricata*, and *Sorbus aucuparia* were observed in all zones, though some, such as *Sorbus aucuparia*, occurred at very low densities along the elevational gradient (see Figure 3 for more details).

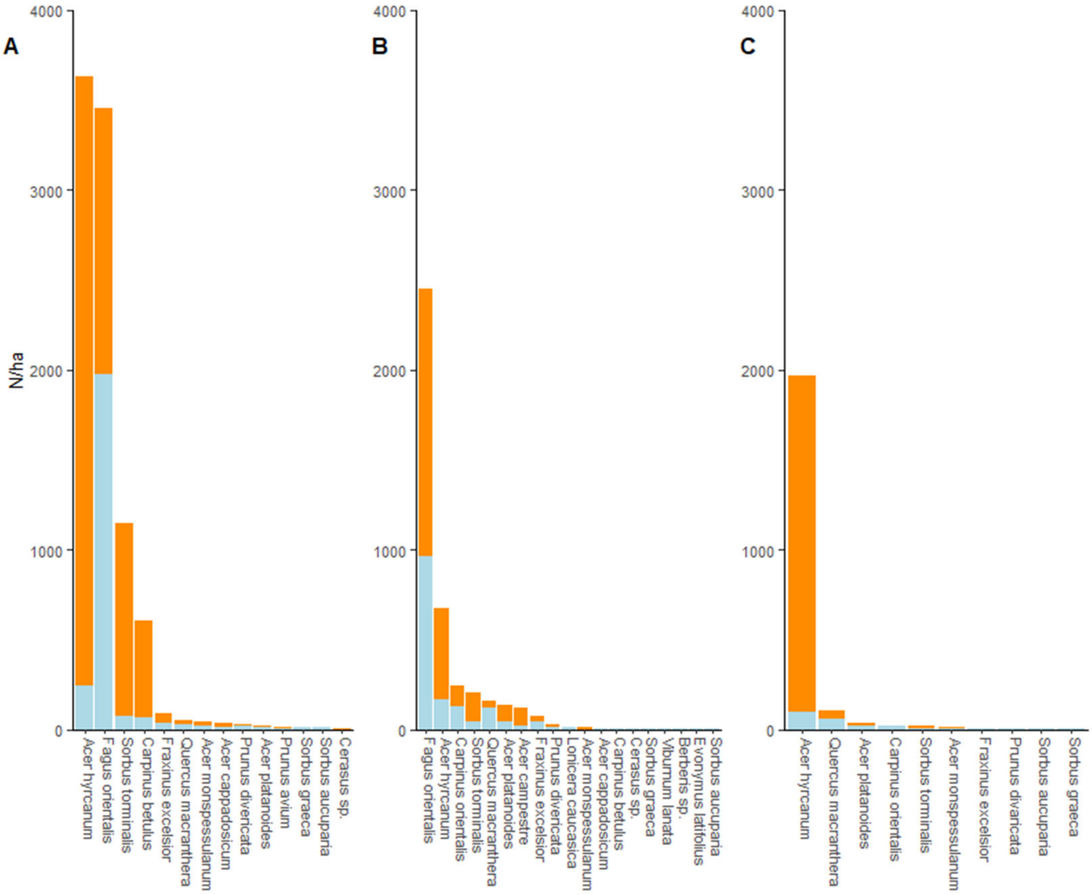

Figure 4. Distribution of seedlings (number per hectare) for each tree species at two life stages: Class I (seedlings 0–<10 cm, orange) and Class II (saplings 10–<50 cm, blue) across elevational zones (**A**): zone A, (**B**): zone B, and (**C**): zone C. The figure illustrates the density variations of each tree species in the different elevational zones.

3.2. *Association of Seedlings with Facilitative Elements, Microhabitat Substrates, and Soil Variables*

Overall, both seedling classes showed stronger associations with facilitative elements, such as rocks, stones, deadwood, and tree cover, than with microhabitat substrates like vegetation and litter. We recorded a notable abundance of seedlings near at least one facilitative element; for example, *Acer hyrcanum* and *Fagus orientalis* were particularly abundant under tree cover (Figure S1).

We observed different correlations between facilitative elements and the two seedling classes, indicating distinct preferences at different establishment stages (Figure 5).

Class I seedlings were positively correlated with deadwood in zones A and B, whereas Class II saplings exhibited a negative correlation with deadwood. Similarly, Class I seedlings showed positive correlations with tree cover in zones B and C, while Class II saplings had negative correlations with tree cover in these zones. In zone C, Class I seedlings were found in sites without any facilitative elements (Table 2), whereas Class II saplings in this zone tended to avoid sites lacking facilitative elements (Table 3).

Seedlings also demonstrated different preferences for microhabitat substrates, though these were less significant compared to facilitative elements. Class I seedlings showed mostly negative correlations with vegetation cover (Table 2), while Class II seedlings were positively correlated with vegetation. Additionally, their relationships with litter varied between the two classes in zones A and B: Class I seedlings were negatively correlated with litter amount, whereas Class II seedlings were positively correlated with it (Table 3).

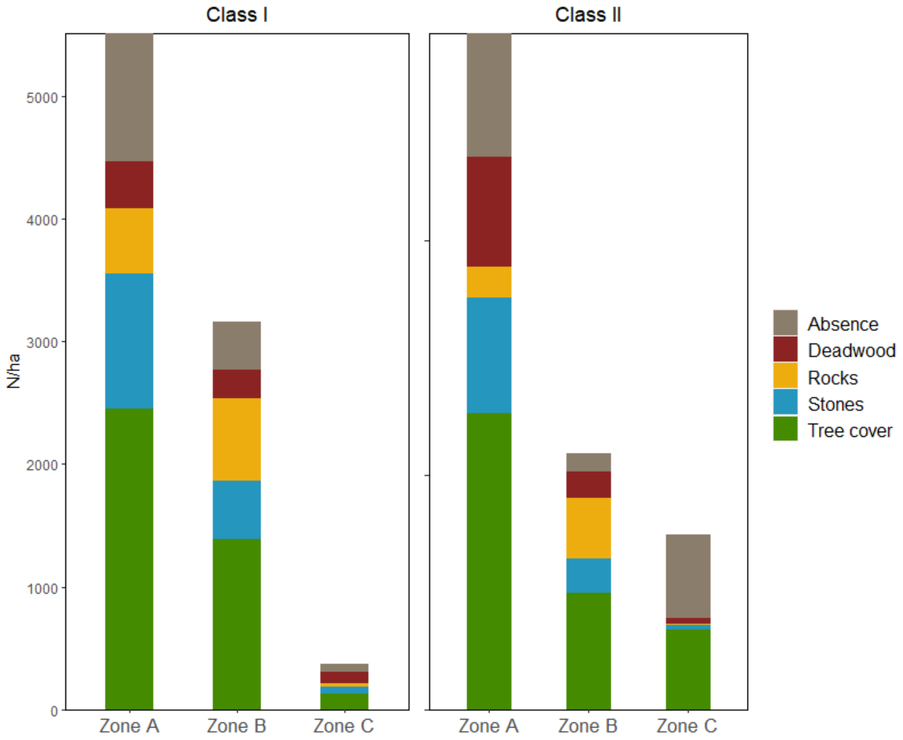

Figure 5. Variation in facilitative elements between two life stages (seedlings and saplings) in zones A, B, and C along the elevational gradient. The figure displays how the presence and type of facilitative elements (such as rocks, stones, deadwood, and tree cover) vary between seedlings (Class I: 0–<10 cm) and saplings (Class II: 10–<50 cm) in different zones.

Table 2. Results of the generalized linear model (GLM) showing the importance of facilitative elements (white rows) and microhabitat substrates (grey rows) for Class I seedlings (0–<10 cm) across different zones along the elevational gradient. Significant predictors are printed in bold.

Facilitative Element	Estimate	Std. Error	z Value	Pr (>|z|)	Chi-Square
			Zone A		
(Intercept)	1.76	0.38	4.68	2.93×10^{-6} ***	
Rocks	−1.01	0.13	−7.59	3.26×10^{-14} ***	59.24 ***
Stones	−0.26	0.15	−1.72	8.47×10^{-2}	3.77
Deadwood	1.26	0.13	9.43	$<2 \times 10^{-16}$ ***	145.78 ***
Tree cover	−0.36	0.26	−1.38	1.69×10^{-1}	0.13
Absence	0.04	0.17	0.23	8.15×10^{-1}	3.73
Vegetation	0.01	0	3.01	2.59×10^{-3} **	13.05 ***
Litter	−0.01	0	−3	2.67×10^{-3} **	24.44 ***
Bare Soil	0	0	0.51	6.08×10^{-1}	0.39
Stones	0	0.01	−0.72	4.72×10^{-1}	0.51
			Zone B		
(Intercept)	−0.37	0.65	−0.58	5.65×10^{-1}	
Rocks	0.63	0.22	2.82	4.81×10^{-3} **	10.08 **
Stones	0.58	0.23	2.53	1.15×10^{-2} *	1.45
Deadwood	0.62	0.17	3.58	3.47×10^{-4} ***	8.69 **
Tree cover	1.69	0.27	6.21	5.21×10^{-10} ***	0.03 ***
Absence	0.31	0.26	1.2	2.30×10^{-1}	45.85
Vegetation	−0.05	0.01	−7.05	1.78×10^{-12} ***	61.38 ***
Litter	−0.01	0.01	−2.12	3.38×10^{-2} *	6.87 **
Bare Soil	−0.01	0.01	−1.39	1.66×10^{-1}	1.14
Stones	−0.01	0.01	−0.94	3.49×10^{-1}	0.89

Table 2. *Cont.*

Facilitative Element	**Estimate**	**Std. Error**	**z Value**	**Pr (>|z|)**	**Chi-Square**
		Zone C			
(Intercept)	0.34	0.79	0.44	6.63×10^{-1}	
Rocks	0.17	0.59	0.28	7.81×10^{-1}	25.13 ***
Stones	0.03	0.44	0.08	9.40×10^{-1}	39.08 ***
Deadwood	−0.47	0.49	−0.97	3.32×10^{-1}	47.34 ***
Tree cover	0.73	0.3	2.46	1.38×10^{-2} *	19.03 **
Absence	3.15	0.62	5.11	3.20×10^{-7} ***	7.32
Vegetation	−0.03	0.01	−4.98	6.27×10^{-7} ***	51.49 ***
Litter	0.01	0.01	1.53	1.27×10^{-1}	2.53
Bare Soil	0	0.01	0.26	7.96×10^{-1}	0.03
Stones	0	0.01	0.29	7.69×10^{-1}	0.09

*, ** and *** indicate statistical significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels, respectively.

Table 3. Results of the generalized linear model (GLM) showing the importance of facilitative elements (white rows) and microhabitat substrates (grey rows) for Class II saplings (0 < −50 cm) across different zones along the elevational gradient.

Facilitative Element	**Estimate**	**Std. Error**	**z Value**	**Pr (>|z|)**	**Chi-Square**
		Zone A			
(Intercept)	−1.76	0.38	−4.68	2.93×10^{-6} ***	
Rocks	1.01	0.13	7.59	3.26×10^{-14} ***	59.24 ***
Stones	0.26	0.15	1.72	8.47×10^{-2}	3.77
Deadwood	−1.26	0.13	−9.43	$<2 \times 10^{-16}$ ***	145.78 ***
Tree cover	0.36	0.26	1.38	1.69×10^{-1}	0.13
Absence	−0.04	0.17	−0.23	8.15×10^{-1}	3.73
Vegetation	−0.01	0.00	−3.01	2.59×10^{-3} **	13.05 ***
Litter	0.01	0.00	3.00	2.67×10^{-3} **	24.44 ***
Bare Soil	0.00	0.00	−0.51	6.08×10^{-1}	0.39
Stones	0.00	0.01	0.72	4.72×10^{-1}	0.51
		Zone B			
(Intercept)	0.37	0.65	0.58	5.65×10^{-1}	
Rocks	−0.63	0.22	−2.82	4.81×10^{-3} **	10.08 **
Stones	−0.58	0.23	−2.53	1.15×10^{-2} *	1.45
Deadwood	−0.62	0.17	−3.58	3.47×10^{-4} ***	8.69 **
Tree cover	−1.69	0.27	−6.21	5.21×10^{-10} ***	0.03 ***
Absence	−0.31	0.26	−1.20	2.30×10^{-1}	45.85
Vegetation	0.05	0.01	7.05	1.78×10^{-12} ***	61.38 ***
Litter	0.01	0.01	2.12	3.38×10^{-2} *	6.87 **
Bare Soil	0.01	0.01	1.39	1.66×10^{-1}	1.14
Stones	0.01	0.01	0.94	3.49×10^{-1}	0.89
		Zone C			
(Intercept)	−0.34	0.79	−0.44	6.63×10^{-1}	
Rocks	−0.17	0.59	−0.28	7.81×10^{-1}	25.13 ***
Stones	−0.03	0.44	−0.08	9.40×10^{-1}	39.08 ***
Deadwood	0.47	0.49	0.97	3.32×10^{-1}	47.34 ***
Tree cover	−0.73	0.30	−2.46	1.38×10^{-2} *	19.03 **
Absence	−3.15	0.62	−5.11	3.20×10^{-7} ***	7.32 ***
Vegetation	0.03	0.01	4.98	6.27×10^{-7} ***	51.49 ***
Litter	−0.01	0.01	−1.53	1.27×10^{-1}	2.53
Bare Soil	0.00	0.01	−0.26	7.96×10^{-1}	0.03
Stones	0.00	0.01	−0.29	7.69×10^{-1}	0.09

*, ** and *** indicate statistical significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels, respectively.

Seedlings at the two different life stages showed distinct associations with soil variables. In the uppermost zone (zone C), seedlings of both classes were positively correlated with nitrogen content. However, Class I seedlings also showed relationships with sand and bulk density (Table 4).

Table 4. Importance of soil variables on seedlings and saplings at two establishment stages: Class I (0–<10 cm) and Class II (10–<50 cm) per zone along the elevation transect. The table details how different soil variables influence seedling and sapling densities in each zone.

Soil Factors	Estimate	Std. Error	z Value	Pr (>∣z∣)	Chi-Square	Estimate	Std. Error	z Value	Pr (>∣z∣)	Chi-Square
	Class I					Class II				
					Zone A					
(Intercept)	7.92	2.81	2.82	4.87×10^{-3} **		−2.53	3.5	−0.72	0.47	
N	−14.85	11.84	−1.25	0.21	4.24 *	25.94	14.73	1.76	0.08	0.09
Sand	4.49×10^{-3}	0.02	0.27	0.79	0.99	0.03	0.02	1.32	0.19	4.04 *
Bulk density	2.15	1.4	1.53	0.13	2.14	3.41	1.75	1.95	0.05	3.89 *
					Zone B					
(Intercept)	7.28	2.24	3.25	1.17×10^{-3} **		7.44	2.1	3.54	3.99×10^{-4} ***	
N	1.73	9.93	0.17	0.86	1.10	3.37	9.3	0.36	0.72	0.38
Sand	0.05	0.02	3.19	1.40×10^{-3} **	5.60 *	0.03	0.02	1.88	0.06	0.46
Bulk density	−1.74	0.81	−2.14	0.03 *	6.11 *	−1.37	0.76	−1.8	0.07	4.51 *
					Zone C					
(Intercept)	−0.21	2.71	−0.08	0.94		−0.21	2.71	−0.08	0.94	
N	66.18	16.19	4.089	4.34×10^{-5} ***	34.01 *	66.18	16.19	4.09	4.34×10^{-5} ***	7.75 **
Sand	−0.03	0.02	−1.65	0.1	1.84	−0.03	0.02	−1.65	0.1	466.3 ***
Bulk density	−0.82	0.52	−1.57	0.12	0.91	−0.82	0.52	−1.57	0.12	5.46 *

*, ** and *** indicate statistical significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels, respectively.

4. Discussion

Our analyses in the Alborz Mountains revealed significant variation in life stage preferences for site factors. As in other high-elevation sites (e.g., [6]), the preferences change throughout the life history, from small seedlings to young saplings. One-year-old seedlings (Class I) correlated with tree cover, consistent with findings from other studies (e.g., [42]). Tree cover supports regeneration by providing microclimatic benefits such as protection from direct solar radiation and wind [43]. Unexpectedly, Class II saplings occur on sites with less tree cover. While tree cover is expected to protect against solar radiation and facilitate sapling growth [44], dense tree cover can limit light availability [45,46], which is essential for light-demanding species such as *Acer hyrcanum* and *Quercus macranthera*. In zones B and C, where the canopy is less dense than in zone A, and sunlight is expected to be sufficient, tree cover had a negative effect. A possible explanation could be competition for nutrients between saplings and mature trees [47,48]. In the upper zones, especially zone C, we observed primarily old trees (compared to the number of seedlings and saplings). Their larger and deeper root systems may limit nutrient availability for Class II saplings, which are expected to require more nutrients than seedlings. However, the impact of below-ground competition on shade tolerance remains an open question that requires further laboratory and field experiments [49]. In addition to tree cover, other environmental factors such as deadwood are important for seedling survival. Deadwood is a crucial shelter element for seedlings in treeline environments, as exemplified in a treeline ecotone in the Himalayas, Nepal [5]. Seedlings associate with deadwood because it provides safe microsite and nutrition conditions and protects against high radiation, high temperatures, wind, and soil moisture deficits [5,50–52]. These factors are particularly important for Class I seedlings, which may need extra protection from drought, water stress, and grazing by domestic animals after germination [53–55] The ecological role of deadwood for later life stages may be different. For instance, a study in northern Japan found that coarse woody debris was useful for seedbed, but its water extracts were acidic and low in nutrients [56]. Thus, nutrient supply from deadwood may not always be sufficient for later life stages.

The high association of both seedling classes with rocks and stones indicates their important functions in stabilizing the soil, regulating day and night temperatures, mediating UV radiation and wind speed, and providing additional water in cracks and crevices [57]. Rocks and stones can play a significant role when acting as physical barriers to protect seedlings and saplings from herbivores.

In addition to these protective properties, interactions with microhabitat substrates also contribute to seedling survival and growth. Although, the association of seedlings with different microhabitat substrates was generally lower than with facilitative elements, the two classes still showed distinct correlations with these substrates. The positive correlations of seedlings with vegetation cover confirm the role of herbs in enhancing seedling and sapling survival [58,59]. Vegetation cover provides physical barriers that protect seedlings from harsh environmental conditions such as wind and excessive sunlight and helps reduce moisture loss [60]. However, the negative effects of herbs on Class I seedlings may be due to competition for water, similar to findings for *Quercus faginea* seedlings [61]. Interpreting these complex interactions is challenging. For instance, Facelli and Pickett [62] demonstrated that litter indirectly promotes the establishment of woody seedlings by reducing herb competition. They observed a strong negative effect of herb competition and a positive indirect effect of litter on woody seedling establishment. Interestingly, our study found both positive and negative effects of litter on seedlings and saplings, highlighting the preferences associated with different establishment stages [5,6]. These contrasting effects highlight the need for a deeper understanding of how litter affects seedling dynamics at different life stages. For example, litter may benefit Class II seedlings by potentially retaining soil moisture, protecting the soil, and providing better nutrient availability [60,63,64]. The same may be true for saplings; however, thick layers of litter, as observed in zones A and B with closed canopies and correspondingly more litter, may inhibit root development and prevent seeds from reaching the soil [62]. The relationships between litter and seedlings/saplings found in this study suggest that future research should investigate how litter and vegetation cover directly and indirectly influence abiotic conditions and biotic interactions related to seedling and sapling growth [5].

While safe sites may enhance seedling establishment, environmental factors such as soil variables also contribute to seedling establishment. Nitrogen is one of the most crucial nutrients for plants [65], and both seedling classes showed correlations with it. Additionally, Class I seedlings were mostly correlated with factors that mediate access to water or root growth, such as their association with bulk density and the percentage of sand. In the upper zones, high bulk density, also noted by Kooch et al. [66] in the Hyrcanian forests, impedes plant root penetration, reducing water flow and air capacity [67]. Such soils require more energy for seedlings to develop their root systems. Similarly, sand improves soil drainage and allows oxygen to reach the roots, which is beneficial for root respiration and nutrient uptake [68]. However, the naturally low water-holding capacity of sandy soils makes them susceptible to drought, which could lead to drought stress in seedlings [69].

Considering the distribution of seedlings along the elevational gradient, the density of seedlings is not comparable between zone A and zones B and C, especially for Class II. Our study area is part of the upper montane/subalpine forest, which is dominated by *Fagus orientalis*, *Acer hyrcanum*, *Quercus macranthera*, and *Carpinus betulus* [26]. Accordingly, seedlings of these species occurred at higher frequencies compared to other tree species. We found a remarkable number of seedlings of *Acer hyrcanum* and *Fagus orientalis*, much higher than the number of seedlings of the other two dominant species in these forests, and especially higher than the number of seedlings of *Quercus macranthera*, which dominates the upper forest edge. *Fagus orientalis* is known for its high regeneration under closed canopy in Hyrcanian forests [70,71]. As our study showed, the number of seedlings of this species was still high in zone B, where the canopy is not as closed as in zone A. In zone C, many *Acer* *hyrcanum* Class I seedlings occur; the high number of Class I seedlings could be the result of a particular year of mast seed production which can occur at irregular intervals [72]. Seed masting can facilitate cohort recruitment success and might be responsible for the increased proportion of Class I seedlings. However, the occurrence of earlier seeding years may have potentially a cascading effect, leading to a higher number of Class II saplings in subsequent years. However, the number of class II saplings is low compared to class I, indicating the mortality of many Class I seedlings in the second year. *Acer hyrcanum* is a drought-tolerant and light-demanding species [73], known to form plant communities with *Quercus macranthera* at high elevations in the Alborz Mountains [23,25]. Except for the high number of *Acer hyrcanum* seedlings in zone C, the low seedling availability at the upper elevational limit of tree growth may be due to the following reasons: (i) low reproduction of well-adapted species, such as *Quercus macranthera*, as even the number of Class I seedlings was not high; or (ii) less successful establishment of trees in areas where climatic conditions are not a limiting factor [19], with establishment potentially being strongly related to shelter elements such as tree shading and rock or stone cover. We did not analyze the effect of grazing on seedling establishment, but the reduced occurrence may be related to the higher grazing rate in upper zones compared to zone A [74]. Therefore, the presence of shelter elements that protect seedlings and saplings from grazing becomes more important. Studying the success of dispersal and establishment in response to grazing can shed more light on the future successful regeneration of trees, which is a basic prerequisite for the presumed upslope migration of trees in response to climate warming.

Here, we present the responses of seedlings from all tree species along the elevational gradient while neglecting species-specific responses. Although tree species are predicted to have different preferences ([5,6]; see Table S1 for more information on the responses of common tree species in the study area), we observed a remarkably high richness of tree species at the upper limit of tree growth in the Alborz. Consequently, more data are needed to test theories on safe site conditions and environmental variables for each tree species. Such data would provide further evidence on the potential upward movement of tree species in response to future climate warming.

5. Conclusions

In this study, we investigated the dependence of seedling recruitment on site conditions and the role of soil variables in influencing seedling density in the Alborz Mountains. Our findings reveal a stronger association of seedlings with facilitative elements, such as tree cover, deadwood, and stones, compared to microhabitat substrates. Small seedlings were particularly dependent on tree cover, deadwood, and stones, while saplings tended to avoid tree cover and deadwood. Stones provided beneficial conditions for both seedling classes, likely offering protection against grazing by domestic animals. Despite the expected benefits of tree cover for young seedlings, root competition, especially at high elevations, appears to limit seedling establishment.

We conclude that the potential upslope migration of trees in response to climate warming in the Alborz depends on the availability of safe sites for small seedlings and saplings. However, other factors, such as seed dispersal, nutrient competition, and space, should also be considered when assessing tree expansion in the context of future climate change.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15111952/s1, Figure S1: Variations in facilitative elements for the two seedling establishment stages: Class I (0–<10 cm) (the upper panels) and Class II (10–<50 cm) (the lower panels) for the most dominant tree species in the study area, summarized separately for elevation zones A, B, and C; Table S1: Results of the GLM for common tree species in the study area, showing the importance of facilitative elements and microhabitat substrates for all seedlings and saplings (0–<50 cm) in different zones along the elevational gradient.

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Data Availability Statement: The datasets generated during the current study are available from the first author upon reasonable request.

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