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Original article

Do environmental variables and overstory communities affect the spatial pattern of understory vegetation? Lessons from *Monotheca buxifolia* (Falc.) A. DC. forests in Pakistan

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ABSTRACT

The importance of understory vegetation cannot be denied as an integral component of forest ecosystems, but there is a dearth of studies to explore the effects of environmental variables and canopy species on its diversity and composition. Here we investigated the effects of environmental variables and overstory stand structure on the understory vegetation in old-growth *Monotheca buxifolia* dominated forests with considerable co-dominance of other broadleaved by using ecologically standardized data collection methods across Pakistan. Multivariate analyses were used to examine the vegetation composition and different species assemblages with multiple influencing variables. We found a total of 58 understory species belonging to 55 genera and 30 families mostly representing pluriregional (33.89 %) chorological affinities with therophytic (17 species) life-form dominance and microphyll (34.48 %) leaf-size spectrum. Likewise, significant differences were observed in species richness and diversity indices between different understory community types. Attributes such as elevation, aspect, soil properties, and tree canopy structure were most strongly correlated with the Redundancy Analysis (RDA-ordination), indicating that several factors exert the strongest influence and explained the spatial pattern of understory vegetation. The findings of this research can assist forestry resources managers, forest biologists and ecologists in restoration and conservation plans for understory vegetation in the region.

Keywords: canopy species, redundancy analysis, floristic composition, edaphic variables, Community types

Introduction

The complex interaction among individuals of different species and several environmental components leads to spatial diversities in plant species communities (Márialigeti *et al*. 2016; Ullah *et al*. 2021). Vegetation-environmental relations are scale-dependent (Qiu *et al*. 2013; Huo *et al*. 2014) and largely influenced by certain environmental factors such as topographic variables (elevation, slope, aspect), soil

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features, and stand condition at a local scale (Cheng *et al*. 2021; Deák *et al*. 2021), but at a regional scale, the role of climatic variables are more significant (Jarvis *et al*. 2013). Microclimate and resource availability below the tree canopy can also be heavily affected by topography (Koorem & Moora 2010; Dölle *et al*. 2017), which leads to the diversification of understory floral composition and diversity. Likewise, the topography has highly influenced the distribution of plant species (Khan *et al*. 2015), due to its linkages with other factors (e.g., light intensity, precipitation, and soil physio-chemical properties) which directly affect plant accessible resources like, soil moisture, and nutrients (Carboni *et al*. 2010; Yu & Sun 2013). The effects of the aforementioned variables are of major importance for the species distribution and normal functions of its life cycle (Ullah *et al*. 2020) apart from field management, natural and anthropogenic disturbances (Khan *et al*. 2013; Ullah *et al*. 2021).

Understory vegetation is highly important in sustaining forest ecosystems composition, structure, and function (Augusto *et al*. 2003; Mölder *et al*. 2008), easing energy flow, nutrients cycle, and supporting the canopy development as a forest ecosystem driver (Nilsson & Wardle 2005). Although the understory flora shares comparatively less to the total forest plant biomass (Gilliam 2007), it explains a major part of the floral diversity (Roberts & Gilliam 2003; Bartels & Chen 2010). Moreover, understory vegetation with a varied range of species promotes forest structural complexity and also provides habitat and energy for other organisms, thereby increasing its diversification (Dauber *et al*. 2003). The understory flora is also predominantly significant to forest natural regeneration (Jouveau *et al*. 2020), as it has a visible effect on the germination process, survivability, and development of juveniles, due to resources limitation (Augusto *et al*. 2003; Messier *et al*. 2008). In this sense, extra focus has been given recently to the forest's understory flora and factors affecting its structure, composition, and distribution which are vital for environmental maintenance and forest protection (Bartels & Chen 2010; Yu & Sun 2013).

The importance of canopy species for the understory plant diversity and composition was reported by several studies (Qian *et al*. 2003; Dölle *et al*. 2017) focusing on stand management (Huo *et al*. 2014), natural and anthropogenic intervention (Ababou *et al*. 2009), light resources (Ameztegui *et al*. 2012; Lefrancois *et al*. 2008), litter properties (North *et al*. 2005; Ellsworth *et al*. 2004), soil nutrients and pH (Hart & Chen 2006; Chávez & Macdonald 2010). Understory flora in different forests has been explained by several workers (Tuanmu *et al*. 2010; Kendrick *et al*. 2015; Dölle *et al*. 2017) and is considered as a biodiversity hub with a variety of shrubs, herbs, and grasses (Barbier *et al*. 2008). In pure broadleaved forests, the availability of resources is more similar in comparison to mixed stands, which are useful tools for diversity in the understory vegetation (Xie *et al*. 2021), and are more crucial for water maintenance and soil conservation (Haughian *et al*. 2017).

Life-form characterizes several adaptive features of a species, and thus it is an appearance of the agreement to the environmental condition of a plant (Parveen *et al*. 2008). Plant life-forms are affected both by genetic and environmental variables since the environment can influence the production of several essential forms of plants. In a specific area, the leading life-form of flora highlights the way that plants have adapted to that region (Mavhura & Mushure 2019). The adaptation of a plant to certain ecological conditions determines a life-form; therefore, it is an important physiognomic characteristic that has been widely used in the analysis of vegetation (Al-Sherif *et al*. 2013). Life-form is the indicator of micro and macroclimate and it is characterized by plant adaptation to certain ecological conditions (Qureshi & Bhatti 2010). Until now, several procedures have been adopted to classify plant life-forms, in which Raunkiaer's system is more acceptable (Azizi & Keshavarzi 2015).

The diverse climate and rough terrain of Pakistan support the vegetation with almost 6000 documented vascular plant species (Gulzar *et al*. 2019). The country's northern regions are considered biodiversity hubs with 42 % of the recorded flora, representing the multiplicity of the sub-region in the Sino-Japanese phytogeographical region of the world (Sher *et al*. 2014; Rahman 2016). Climatic variability is the possible reason for such richness and diversity and is predominantly linked to the altitudinal gradients of the area (Ullah *et al*. 2021). In Pakistan, major species of the broad-leaved forests are *Olea ferruginea*, *Quercus baloot*, *Acacia modesta*, *Monotheca buxifolia*, and *Punica granatum* (Khan *et al*. 2015). Among them, *M. buxifolia* is a wild, fruit yielding broadleaved tree species providing many services to the rural and urban inhabitants. So far, studies on different aspects of this commercially and ecologically important tree species have been conducted (Khan *et al*. 2011; Ali *et al*. 2022a), but no work has been carried out yet to investigate the understory diversity, composition, underlying structure, and its influential factors. Furthermore, the tree's canopy effects in these forests are still ignored. Therefore, this study investigated the understory vegetation with environmental variables and structural attributes in 44 stands across Pakistan. We hypothesized that understory species composition and diversity would differ significantly because of varied topographic, edaphic, and overstory composition and structure. Additionally, we aimed to explore which environmental variables and forest stand factors could explain the variation in understory species composition in *M. buxifolia* dominated forests in the region.

Materials and Methods

Study Area

The effect of different variables including edaphic, topographic, and canopy of woody trees on the understory vegetation of *M. buxifolia* dominated forests were studied at different localities across Pakistan, during the period from 2018 to 2019 (Fig. 1). Pakistan is a south Asian country spreads over 80,943 km^2, spinning between 60° 55' to 75° 30' longitude and 23° 45' to 36° 50' latitude (Ali *et al*. 2022a). Uneven topography, undulant valleys, diverse slopes, hillocks, huge mountains, plains, and many water streams joining main rivers are the basic structures of the studied area. Pakistan has a diverse climate and biodiversity due to the elevation gradient ranging from the sea level to 8,611 m with more than 6000 identified plant species (Ali & Qaiser 1986). The hotspot flora of the studied area is distributed in thirteen natural regions *i.e.*, Alpine pastures to Mangroves, where the endangered flora is >10 % (Shinwari 2011). *M. buxifolia* forests are generally distributed at diverse elevation ranges and are often found toward the north and west of the country (Ali *et al*. 2022b).

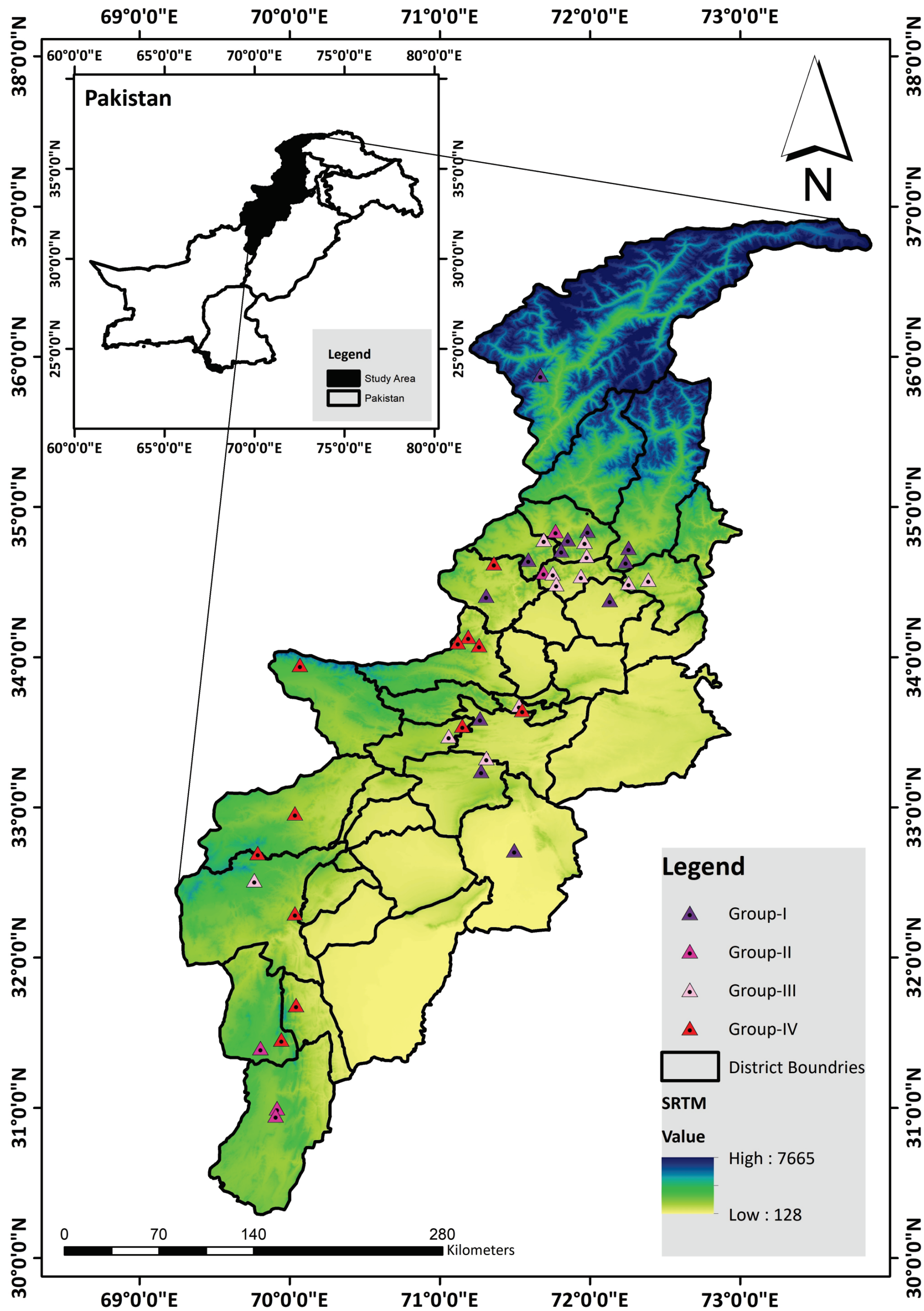

Figure 1. Map display 44 sampling locations of *M. buxifolia* dominated forests in different elevation ranges across Pakistan.

Data Collection

Data on the topographic and edaphic variables, canopy species, and understory vegetation were collected from least disturbed *Monotheca* forests (area ≥ 1 hectare) across Pakistan (Ali *et al*. 2017). We established 10 plots each of 15 m × 15 m = 125 m^2 in 44 forests for vegetation survey at elevation ranges from 647.09 m to 1789.48 m (asl) across the natural distribution range of *Monotheca* in Pakistan. In every sampling plot, the individual tree with a girth of more than 5.0 DBH cm (1.3 m above ground level) was measured, and height was obtained (Ali *et al*. 2019). Density (ha^{-1}) and total tree basal area (m^2 ha^{-1}) for the tree species were calculated in each site. For understory vegetation (shrubs, herbs, and grasses) measurement, 15 m × 15 m plot was then randomly divided into two 5 m × 5 m = 25 m^2 quadrats (Wulf & Naaf 2009). Within a plot, ecological parameters such as density, cover and height for individual plant species were recorded (Russel & Flower 1999). Before the vegetation sampling, information like slope angle (Santo clinometers), aspect (compass), altitude (altimeter), geographical coordinator (GPS), and the presence of natural and man-made interference were documented. Three soil samples in replicates (10-30 cm depth) were arbitrarily collected from the individual plot with a stainless cylindrical steel soil sampler of 5 cm in diameter. The soil samples of each stand were then thoroughly mixed to form a composite sample for further analysis. Soil pH was measured in a 1:2.5 soil to water ratio suspension (Du *et al*. 2010). The volumetric ring method was used to determine the soil bulk density (Zhu *et al*. 2009).

Laboratory Analysis

Botanical samples were collected from all individual trees, shrubs, and herbs in each plot and identified at the Botanical Garden & Herbarium (BGH) University of Malakand. The flora was classified into different life-form, and leaf-size classes following Raunkiaer (1934). The phytosociological attributes (*i.e.*, relative frequency, relative density, and relative basal area) and absolutes values (*i.e.*, stem density ha^{-1} and basal area m^2 ha^{-1}) of all woody species were obtained for individual stands. From the relative values of phytosociological attributes, we calculated an Importance Value Index (IVI) for each tree species following Khan *et al*. (2015). Similarly, the IVI for herbs and shrubs was also calculated using the formula described by Huo *et al*. (2015). We evaluated the data for plant taxonomic composition, Simpson's Index (1/C) and Shannon-Wiener Index (H) to calculate species richness and alpha diversity for each understory community across the four distinct forest vegetation types. One-way ANOVA following Tukey's HSD test was performed to report the differences in species richness and diversity of the understory vegetation between the forest types. Soil physicochemical properties were measured in the laboratory by using a flame photometer, Kjeldahl apparatus, and Atomic absorption (Liu *et al*. 2009).

The relationships between environmental factors, measured overstory structural components, and understory species were then characterized with redundancy analysis (RDA) (ter Braak 2012; Wu *et al*. 2021). First, we performed a Detrended correspondence analysis (DCA) in order to select whether a unimodal (CCA) or linear (RDA) response curve in ordination analysis should be better. Consequently, DCA gradient length was 12.15 for axis 1, 3.41 for axis 2, and 11.33 for axis 3 with 11.63 % of the total variance in species data; therefore, both RDA and CCA were preferred to use for accurate results as suggested by Lepš & Smilauer (2003), Jongman *et al*. (1995). Our analysis demonstrated that RDA explained 50 % of total variance which was higher than CCA (11.63 %). Thus, we used RDA in the final analysis as a linear interaction between species and environmental variables. Nevertheless, the presence of double zeros strongly affects the RDA with arch effect (Ababou *et al*. 2013). In such a case, an alternative has applied either chord (Orloci 1967) or Hellinger (Rao 1995) distance transformation. Tsai *et al*. (2016) showed that this approach is less sensitive to double zeros and consequently to the arch effect. After several comparisons, we chose the Hellinger transformation followed by an RDA and the most significant variables were determined by using the method Wilk's lambda (De Sá 2007; Jones *et al*. 2008). Finally, four pre-defined vegetation groups (Ali *et al*. 2022b) obtained from Ward's agglomerative clustering techniques were used because they inherit major ecological information and were easily interpretable.

Results

Floristic and chorological affinities

The study resulted in a total of 58 understory species belonging to 55 genera and 30 families (Tab. S2). Lamiaceae and Asteraceae were the major families that contributed with the greatest numbers of plant species *i.e.* 8 species and 7 species respectively, followed by Solanaceae (5 species), Poaceae, and Apocynaceae (4 species each). Microphyll dominated the leaf-size classes and was composed of 20 species (34.48 %), followed by nanophyll, mesophyll, leptophyll, and macrophyll respectively (Fig. 2). Of the total leaf-size classes, aphyllous (2 species, 3.89 %) had contributed the least. Likewise, the biological spectrum shows that Phanerophyte was the leading life-form (32.76 %), followed by Therophyte and Cryptophyte ones (Fig. 3). The chorological affinities of the recorded taxa revealed that 33.89 % species were pluri-regional, ranging their distribution all over the Indian and Mediterranean regions, 30.50 % were bioregional, 20.33 % cosmopolitan and only 15.25 % were monoregional (Fig. 4). Of the total species, 18.64 % were mostly native to the Iranian-Turaian region, 12.71 % were native to Euro-Siberian and 11.68 % were from the Mediterranean phytogeographical region.

Vegetation types

The hierarchical agglomerative clusters of the 58 understory plant species in *M. buxifolia* dominated forests can be interpreted in the context of their habitat characteristic and species associations. The cluster analysis of woody tree species retained 65 % of the floristic data with four groups and 10 % chaining. Group-I comprised 12 stands and 793 individuals, representing the largest number (38 species) of shrubs and herbaceous species and ranked as the richest and diverse group (Tab. 1). This group was dominated by *Dodonea viscosa* (Fig. 5) and *Justicia adhatoda* whereas, *Ziziphus nummularia* (IVI= 8.19±4.2 %), *Perovskia abrotanoides* (IVI= 5.66±4.2 %), and *Gymnosporia Royleana* (IVI = 6.93±4.4) were major associates. The majority of the plants (33 species) in this group occurred with importance

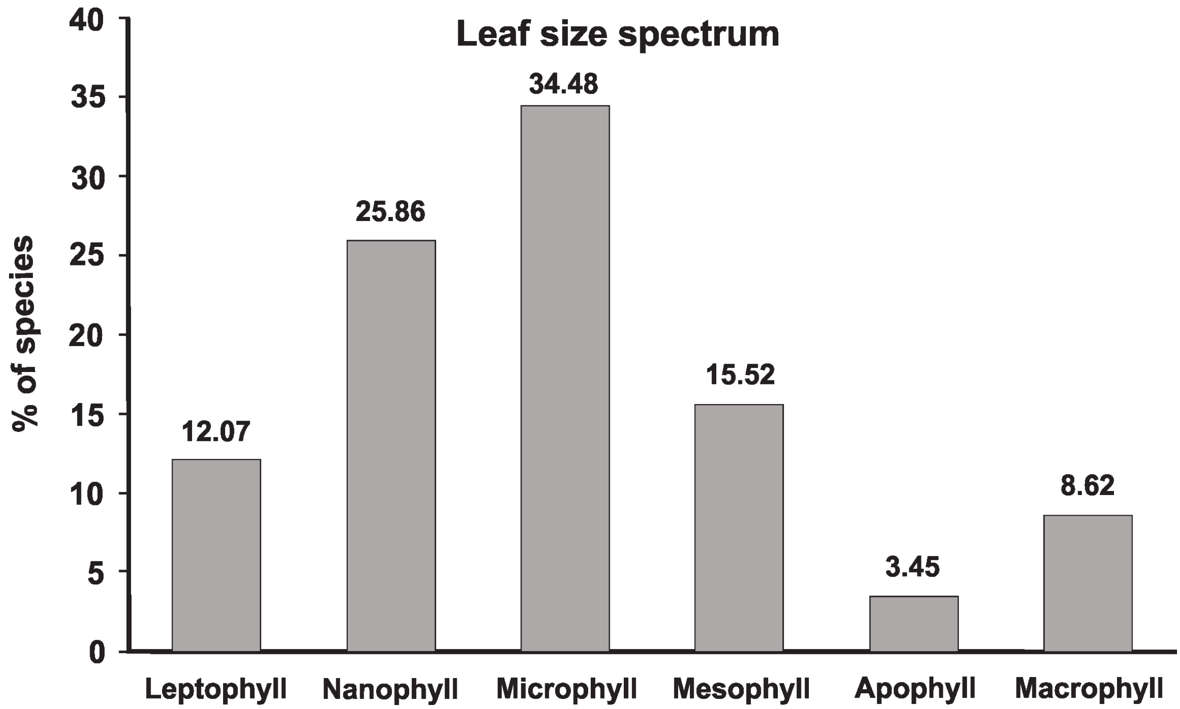

Figure 2. Percent distribution of leaf-size spectrum of understory plant species (*Monotheca buxifolia* dominated forests) found in Pakistan.

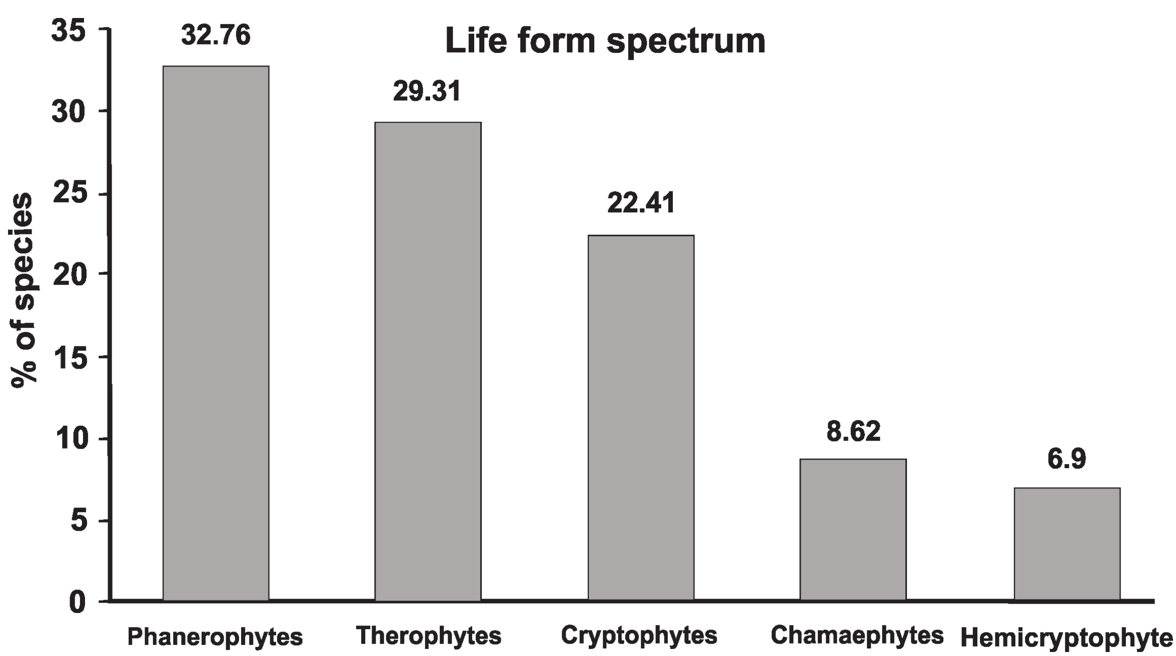

Figure 3. Percent distribution of the understory plant species life-forms in *Monotheca buxifolia* dominated forests in Pakistan.

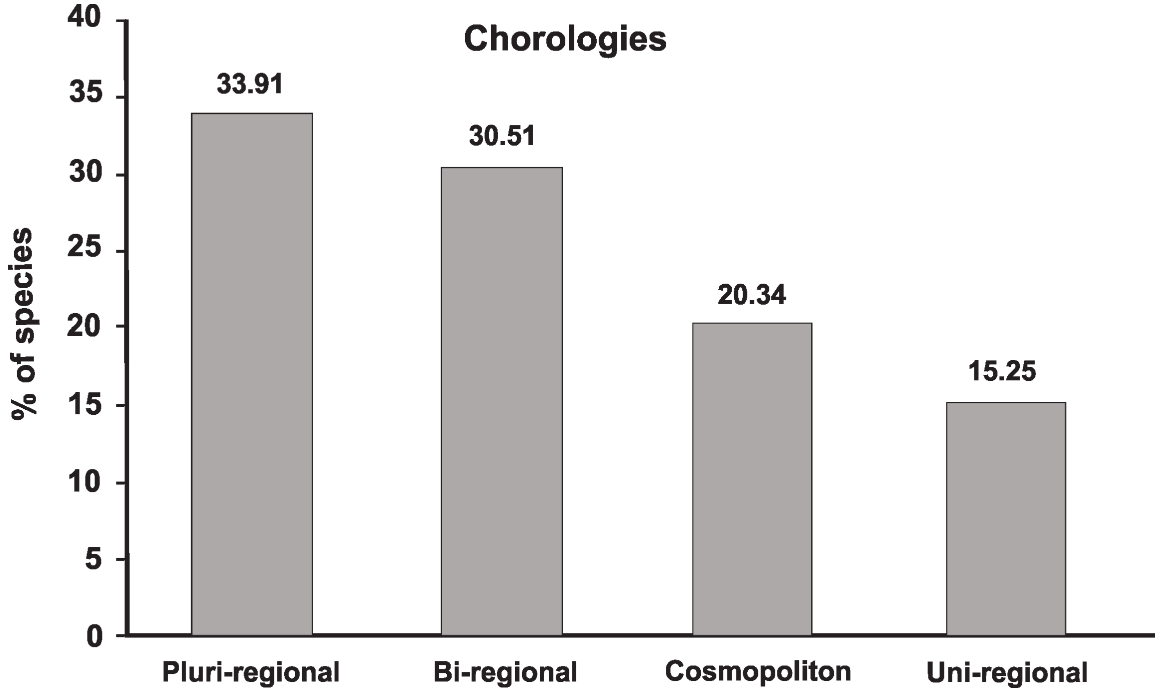

Figure 4. Chorology of understory plant species (%) in *Monotheca buxifolia* dominated forests in Pakistan.

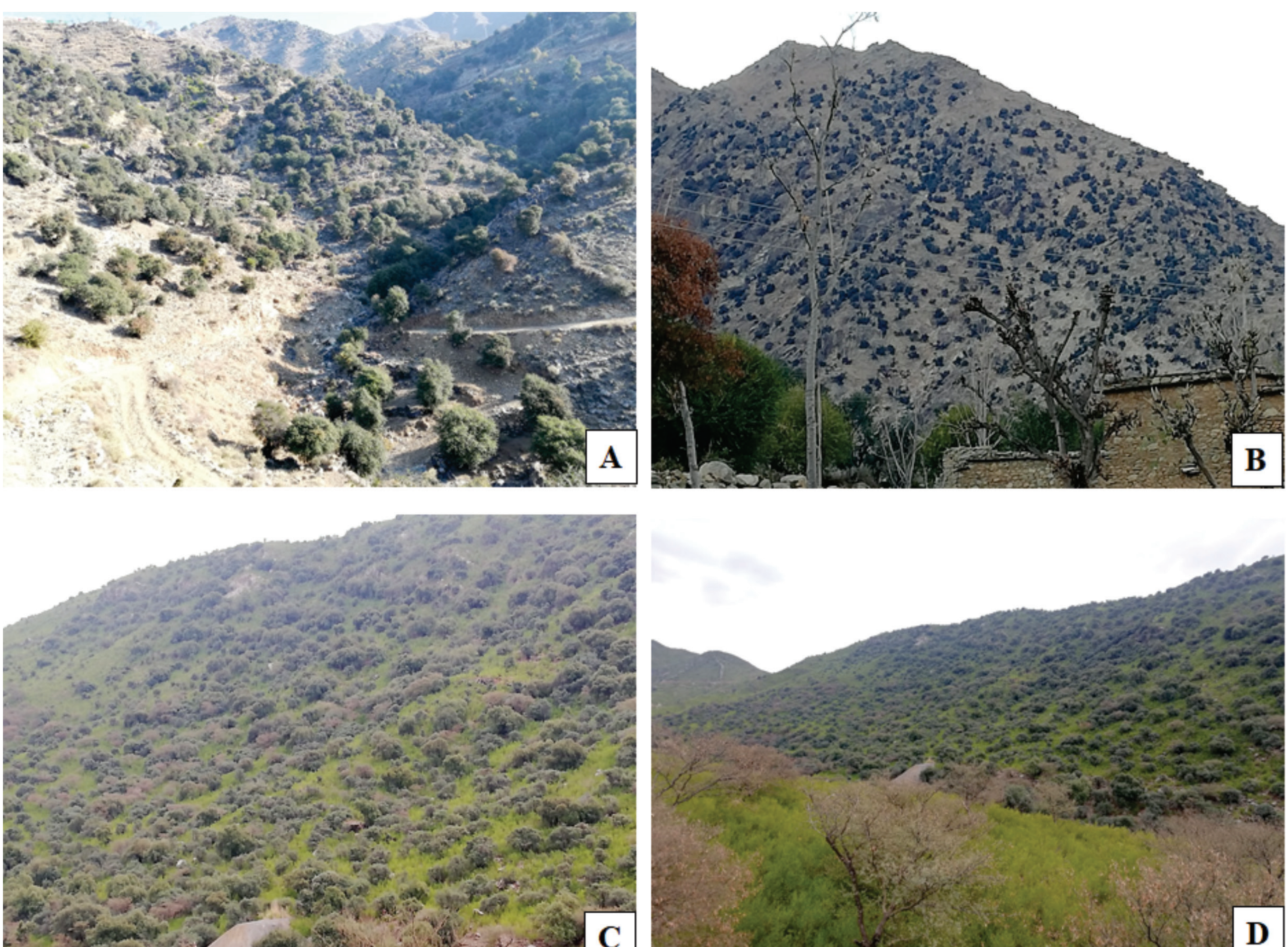

Figure 5. Understory vegetation of *Monotheca* forests; (**A**, **B**) Clear understory vegetation, (**C**, **D**) Understory purely dominated by *Dodonaea viscosa*.

values less than 5 %. This group was different in terms of low elevation (1038.03±68.8 m), slope inclination (21.08±2.85°), high contents of silt, low organic matter, nitrogen, phosphorus, and potassium contents (Tab. 2). Structural attributes such as basal area (53.11±8.5 m^2 ha^{-1}) of *M. buxifolia*, total basal area of the stand (26.91±5.1 m^2 ha^{-1}), and percent Importance value (40.61±1.6 %) were also maximum in this group.

A cluster of six stands (Group-II), with eighteen different species, was reported as the most species-poor and least diverse group (Tab. 1). In this group, large shrubs like *D. viscosa* (IVI= 36.61±17 %), *Withania coagulans* (IVI= 16.67±16 %), and *Nannorrhops ritchiana* (IVI= 13.82±9 %) were dominant. Other common understory species were *Lawsonia inermis* (IVI= 7.42±5.06), *Solanum virginianum* (IVI= 6.57±4.15), and *Carthamus oxyacantha* (IVI= 6.57±4.15). The characteristic features of this group included high elevation (1328±126 m) with a comparatively steep slope (28.5±1.99°). Likewise, lime content (3.04±0.84 %) in the soil was higher; therefore, this group was characterized by high pH (7.9±0.22). Similarly, electrical conductivity (µs/cm) and total dissolved solutes (182.6±17.54) were also higher in this group (Tab. 2). However, the basal area (35.25±5.97 m^2 ha^{-1}) of the dominant overstory species was the lowest, and the total tree basal area (12.56±2.27 m^2 ha^{-1}) was about half of the prior group.

The understory vegetation in group-III was distributed in 12 stands where a total of 479 individuals of shrubs and 26 herbaceous plants were documented. Results of ANOVA exposed a significant difference in species richness of this group in comparison to group-I and II. Further, the difference was confirmed by performing post hoc Tukey's HSD. *D. viscosa* (IVI= 24.6±5.9 %) and *Saccharum munja* (IVI= 10±3.6 %) were the dominant shrubs, whereas *Justicia adhatoda* (IVI 9.2±4 %) and *Plectranthus rugosus* (IVI= 7.5±5 %), were the strong companion in this group.

Table 1. Species richness and diversity indices for the understory vegetation's in *Monotheca* dominated communities resulted from Ward's agglomerative clustering analysis.

Diversity Indices	G1	G2	G3	G4	F	P
Richness (S)	38 [a]	18 [b]	26 [c]	29 [c]	**2.02**	**0.026**
Total no of individuals (N)	793 [a]	183 [b]	479 [c]	249 [c]	**4.04**	**0.013**
Natural log of individuals (ln N)	3.7±0.32 [a]	3.09±0.3 [b]	3.39±0.21 [a]	2.6±0.2 [c]	**3.49**	**0.024**
Simpson's Index (1/C)	3.36±0.53	5.5±3.56	3.38±0.51	2.95±0.49	0.75	0.526
Shannon-Wiener Index (H)	1.3±0.15	0.73±0.23	1.26±0.11	0.95±0.18	1.87	0.149

Table 2. Descriptive statistics of the topographic, soil physiochemical and overstory structural attributes in *Monotheca* dominated forests communities in the study area.

Variables	G1	G2	G3	G4
Latitude (°N)	34.38±0.24	32.77±0.75	34.15±0.21	33.43±0.71
Longitude (°E)	71.74±0.1	64.08±6.54	71.62±0.19	70.79±0.20
Elevation (m)	1038.03±68.8	1328.01±126	1031.72±90	1275.3±80
Slope (°)	21.08±2.85	28.5±1.99	23.25±2.92	26.78±2.65
Aspect	225.75±29.84	203.33±49.8	219.3±24.02	254.93±19.35
Clay (%)	15.12±0.91	15.332.21	14.87±0.87	14.7±0.81
Silt (%)	42.5±3.67	41.61±5.3	41.48±4.01	29.63±2.43
Sand (%)	42.35±4.08	42.98±6.45	43.71±4.24	55.87±2.52
Texture	2±0.21	2±0.25	2.08±0.22	2.35±0.17
pH (1:5)	7.78±0.15	7.98±0.22	7.97±0.11	7.66±0.18
Organic matter (%)	1.03±0.36	1.82±0.72	2.15±0.66	1.52±0.37
Lime (%)	2.15±0.44	3.04±0.84	2.87±1.07	2.73±0.29
Nitrogen (%)	0.056±0.01	0.09±0.03	0.09±0.03	0.067±0.01
Phosphorus (mg/kg)	13.98±1.41	16.77±1.3	15.86±1.34	14.38±1.73
Potassium (mg/kg)	144.25±14.34	149.8±25.7	146.16±18.33	156±15.6
Field capacity	0.25±0.001	0.25±0.01	0.24±0.008	0.23±0.006
Bulk density (g/cm)	1.45±0.015	1.46±0.03	1.46±0.01	1.48±0.01
Available water (%)	0.14±0.006	0.14±0.01	0.13±0.007	0.12±0.004
Electrical conductivity (µs/cm)	282.41±24.99	332±31.9	316.25±25.2	325.07±21.1
TDS	155.32±13.7	182.6±17.54	173.95±13.85	178.79±11.63
Monotheca IVI	59.38±1.64	69.22±2.44	80.87±1.29	97.48±0.97
Total IVI	40.61±1.6	30.77±2.44	19.17±1.29	2.55±0.99
Monotheca basal area	53.11±8.5	35.25±5.97	39.06±8.55	52.61±12.45
Total basal area	26.91±5.1	12.56±2.27	6.56±1.62	1.05±0.56

Note: TDS: Total dissolved solutes; IVI: importance value index

Out of the total understories, 24 plants were below <5% of importance values in this group. Similar to group-I, stands in this group were located at low elevation (1031±90 m), gentle slope (23.25±2.92°), and facing toward the west. The sampled sites in this group were also characterized by low soil pH, high organic matter, potassium, and percent sand contents. The basal area of the dominant species was 39.06±8.55 m^2 ha^{-1} whereas the total tree's basal area was lower than that of group-I and II, respectively.

Alhagi maurorum (IVI= 13.35±7%) and *Calligonum polygonoides* (10.97±5%) dominated the understory vegetation of the group-IV community. *Vitex negundo* and *D. viscosa* were the major associates with the predominant species. As in group-III, a lower number of understories (25 species) were recorded in this group with an importance value of ≤ 5%. Among all the groups, diversity indices, like Simpson's Index (1/C) (2.95±0.49) and Shannon-Wiener Index (H) (0.95±0.18) were recorded least for group-IV (Tab. 1). Stands of this community type were located comparatively at high elevation (1275.3±80 m), slope (26.78±2.65°), and facing north. Among the edaphic variables, silts contents were the least (29.63±2.43), while sand contents (55.87±2.52) dominate the soil texture of this group.

Effect of environmental variables

The RDA ordination shows the stands as diamonds in species space with overlays of the environmental variables and structural attributes as joint plot to reflect the direction and explanatory power of linear relationships with the axes (Fig. 6). We found significant relationships for all redundancy

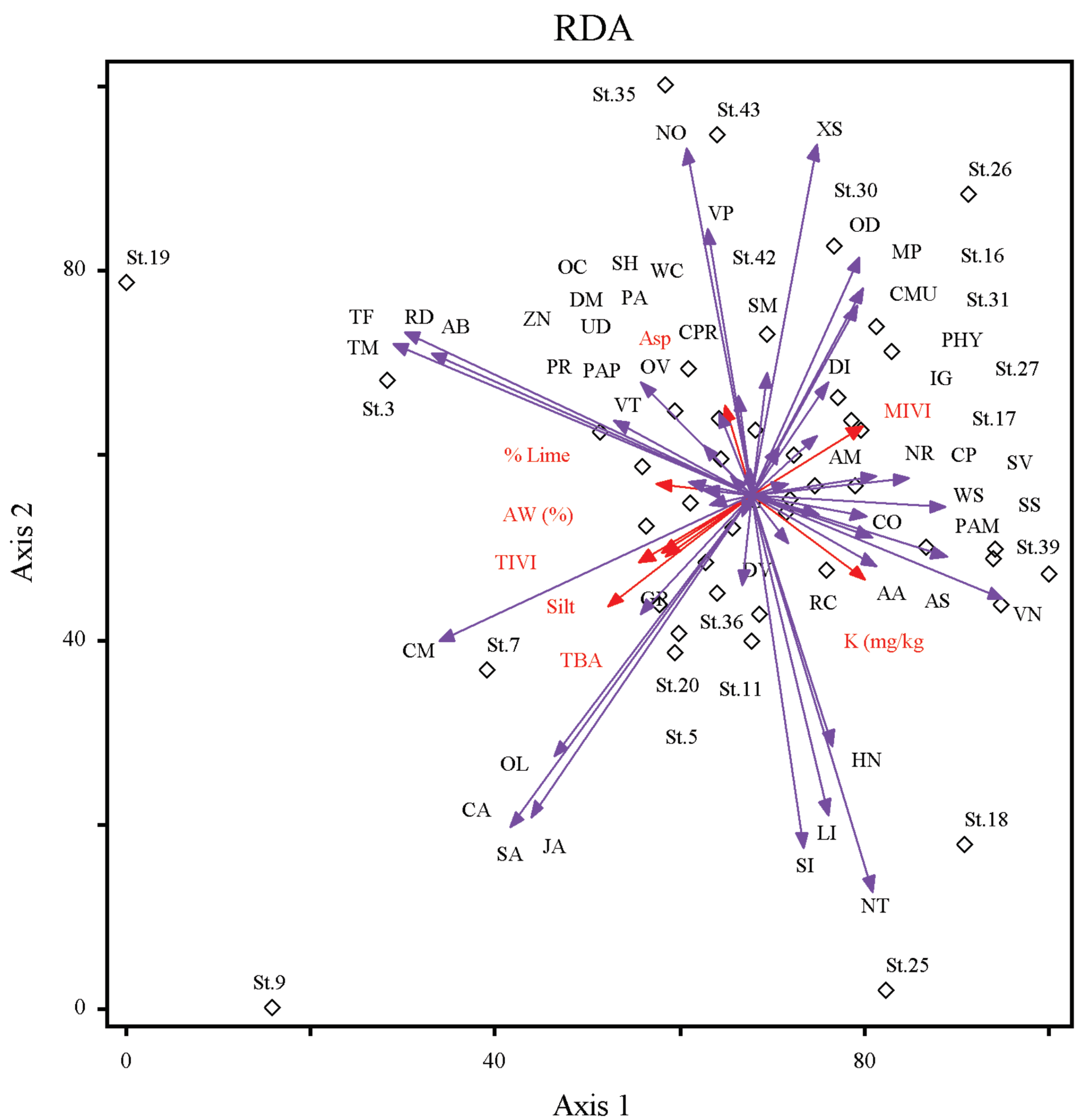

Figure 6. Ordination diagram (RDA-biplot) showing the relationship between 44 *Monotheca* forests (stand ordination) and environmental variables. Species and environmental variables used in the analysis are abbreviated, and full names are shown in Table S2 and Table 2 respectively.

Table 3. RDA-analysis of species-environmental variables operating on the understory vegetation in *Monotheca*-dominated forests in Pakistan.

	Axis 1	Axis 2	Axis 3	P
Eigenvalue (RDA)	3.306	2.581	2.45	0.4104
% of variance explained	6.6	5.2	4.9	---
Cumulative % explained	6.6	11.8	16.7	---
Pearson Corr., Response-Pred.*	0.942	0.932	0.88	---
Kendall Corr., Response-Pred.	0.79	0.743	0.679	---
Monte Carlo test	0.994	0.998	0.993	0.3343

axes, showing that species composition is strongly dependent on environmental factors. Monte Carlo permutation test for RDA ordination indicated that the eigenvalues for axis 1, 2 and 3 were 3.306, 2.581 and 2.45 respectively. The ordination explained 35.1 % of the cumulative variance in the species data by the entire axis (Tab. 3). The first axis has explained 6.6 % of the total variance and positively correlated with potassium, *Monotheca* importance value and negatively correlated with the total basal area (r = -0.512), total IVI (r = -0.403), available water (r = -0.306), Lime (r = -0.344) and silt (r = -0.323) respectively (Tab. S3). The second axis indicated 5.2% of the variance and was significantly correlated with aspect (°) and total tree basal area. The third axis was found to be linked with most of the topographic variables such as elevation (r = 0.549) and slope (r = 0.469). Soil silt, sand, pH, organic matter, and nitrogen were among the edaphic and physicochemical properties affecting understory species composition (Fig. 5; Tab. S3). The values of interest correlation for topographic, edaphic, and overstory vegetation are shown in Table S4.

Discussion

The present study recorded 58 plant species belonging to 55 genera and 30 families. Floristic composition in the studied area is very much affected by local activities and natural regeneration is hindered due to heavy grazing and cutting (Fig. 5). Among all plants, phanerophyte with 32.76 % was dominant and therophyte with 29.31 % was in the next order. In fact, life-forms indicate the possibility of plant adaptations to climatic conditions. The high frequency of phanerophyte is due to cold and temperate climate while therophytic life-form reflects Mediterranean climate (Khan *et al*. 2017). Therefore, the recorded life-form spectrum among the documented understory flora shows the influence of the Mediterranean and cold temperate climate (Azizi & Keshavarzi 2015). The low percentage of hemicryptophytes and chamaephytes shows that they are not adapted to existence climate and edaphic situations. These findings are similar to the results of Floret *et al*. (1990); Schneider *et al*. (2003); Sringeswara *et al*. (2010); and Ullah *et al*. (2015). The leaf-size spectrum shows that microphyllous (34.48 %) species were dominant followed by nanophylls (25.86 %) and mesophylls (15.52 %). Microphylls are symbolic of steppes, whereas nanophylls and leptophylls are representatives of hot deserts (Cain & Castro 1959). Species with large leaves occur in warm moist climates, while smaller leaves represent cold and dry climates (Khan *et al*. 2018). The present study reveals that microphylls and nanophylls were present at high elevations while leptophylls were present at the lower elevation, which is an agreement to findings of Al-Sherif *et al*. (2013). Azizi & Keshavarzi (2015) reported a high percentage of leptophylls and nanophylls in dry subtropical semi-evergreen forests. In our case, a high percentage of microphylls represents the cool climate where the roots absorb low moisture.

The chorological affinities of the recorded flora exposed that understory vegetation of *Monotheca* forests supported plant species with a wide distribution representing several phytogeographical regions of the world. The understory flora of the studied area is distributed in thirteen different regions which are similar to the findings of Ali *et al*. (2017). Phyto-geographically, Pakistan is categorized into 4 major regions: (i) Indian region (6 %), (ii) Saharo-Indian region (9.5 %), (iii) Sino-Himalayan region (10 %), and (iv) Irano-Turanian region (45 % of species) but the maximum number of species in this study were from Irano-Turanian region (18.64 %) followed by Euro-Siberian (12.71 %), which comply the findings of Ali *et al*. (2017).

We found that understory species richness and diversity in the *Monotheca* forests varied significantly with canopy dominants, which is in agreement with various studies (Wang *et al*. 2015; Kobal *et al*. 2015; Echiverri & Macdonald 2020). *Monotheca* dominated forests with a maximum basal area of canopy species have high diversity in understory vegetation. Such a positive impact of canopy species on understory vegetation richness was reported by Chávez & Macdonald (2010). However, several studies report no or weak correlation between the canopy richness and understory vegetation (Dang *et al*. 2018). The effect of canopy species on understory vegetation richness can be linked to multiple environmental variables (Økland 1999). Different other factors, like the level of natural and human hazards, dispersal restrictions, and stochastic events were the most predominant having an adverse effects on vegetation distribution (Berger *et al*. 2004; Nie *et al*. 2019; Kutnar *et al*. 2019). Therefore, understanding the effect of these unexplained factors could be more helpful to describe the mechanisms of species distribution. Elevation coupled with canopy potentially affects the understory floral composition (Yu *et al*. 2013; Rana *et al*. 2011). Soil bulk density and soil slope potentially affect the understory vegetation composition (Echiverri & Macdonald 2020; Piazza *et al*. 2016). In the northern areas of Pakistan, species richness was highly influenced by slope and altitude (Ali *et al*. 2022b; Ullah *et al*. 2020; Qureshi & Bhatti 2010).

Variability of environmental conditions plays an important role in spatial segregation of the flora and structural variations in plant communities (Aikens *et al*. 2007; Huo *et al*. 2015; Dölle *et al*. 2017). In the current work, we identified 4 different groups of understory vegetation based on the importance values of canopy species. Each of these groups possesses different ecological niches in the studied area, representing a unique combination of plant species. Group-I and group-III were dominated by *D. viscosa*, *S. munja*, and *J. adhatoda* preferred the sites of low elevations and gentle slopes. However, group-II and group-IV preferred stands of high elevation having steep slopes. Contrary to group-I and IV, group-II and III appeared to favor slightly basic soil with high contents of soil organic matter. Among the edaphic variables, group-IV was characterized by the high amount of sand content, while stands of group-I favor silty soil. Group-II dominated by *D. viscosa* and *Withania coagulans* was predominantly limited to a high elevation with more clay particles that have an adequate rate of precipitation in the studied area, indicating a mesophyte community. Several studies of vegetation classification were carried out in other high mountain ranges. For example, Huo *et al*. (2015); Siddiqui *et al*. (2016); Muhammad *et al*. (2016), and Ullah *et al*. (2021), classified plant communities of the Himalayas and found that the shrub communities were dominated by *D. viscosa*, *Justicia adhatoda*, *Gymnosporia royleana*, *Berberis lyceum*, *Xanthium strumarium*, and *Indigofera gerardiana*. These results were similar to ours due to the same eco-geographical region.

Our results show that the distribution of the understory vegetation is more likely linked to topography (elevation, slope, and aspect), soil conditions (physical and chemical), and canopy species (Importance value and basal area) as early reported by several workers (Zhang *et al*. 2013; Huo *et al*. 2014; Ali *et al*. 2017; Khan *et al*. 2020; Ullah *et al*. 2021). Not only topography, but the species composition was also heavily affected by soil physicochemical properties due to diverse environmental factors (Ali *et al*. 2017). Altitudes are counted as the most influential factor because it is either directly or indirectly linked with many other environmental elements (for example; precipitation, temperature, humidity, solar radiation, etc.). Previously, several workers (*e.g.*, Khan *et al*. 2015; Huo et al. 2015; Ali *et al*. 2017; Ullah *et al*. 2021), confirmed the effect of elevation on vegetation. High elevation generally leads to an increase in precipitation and solar radiation, but in contrast to this, the relation between temperature and evapotranspiration is inverse (Odland *et al*. 2021). Elevation changes lead to changes in temperature, which influences the growing period of plants (Khan *et al*. 2020), and as a result plant growth and distribution are highly affected.

Soil fertility and moisture are linked to the slope and have a significant impact on spatial changes in plant composition. Low moisture contents in steep slopes of the studied area may be due to thin soil layer and can affect the vegetation adversely (Ali *et al*. 2019; Khan *et al*. 2020). In addition, soil texture, pH, organic matter, nutrients, bulk density, field capacity, and canopy cover were the most significant environmental and vegetation variables affecting floral distribution in this study. A similar effect was also reported in several different studies (*e.g.*, Hou *et al*. 2014; 2015; Dölle *et al*. 2017; Deák *et al*. 2021).

Results of the RDA ordination showed that understory species distributions were significantly influenced by aspect, soil physio-chemical properties, and canopy species, concurring with the findings of previous studies (Huo *et al*. 2014; Ullah *et al*. 2021). Contrary to findings of Augusto *et al*. (2003) and Duguid *et al*. (2013), we reported no effect of soil-based variables like pH, organic matter, bulk density, lime, potassium, and total nitrogen on understory vegetation in our study. However, the importance of aspect and slope on species distribution pattern was described by several workers (Barbier *et al*. 2008; Yu *et al*. 2013), which is in agreement with the findings of the current study. Similarly, Ali *et al*. (2019) also reported a significant effect of topography and edaphic variables on species diversity, richness, and composition in broad-leaved evergreen forests of *O. ferruginea* in the Muslim graveyards of northern Pakistan. The effect of canopy species on understory vegetation was confirmed by RDA in the current study supporting the finding of Koorem & Moora 2010; Ádám *et al*. 2013; Zhang *et al*. 2013).

Conclusions

Understory vegetation holds a large proportion of plant diversity and contributes significantly to ecosystem functioning in forests. In this study, we compared understory vegetation in 4 different *Monotheca* dominated community types. Our findings revealed that each forest type possesses a unique understory community. The leading position of *Monotheca* in the canopy favour changing the understory site conditions significantly, most likely by shading the forest floor and producing a high amount of refractory litter. Results showed that understory species composition was primarily affected by canopy, topography and soil conditions. Comparing explanatory variables, canopy variables (tree basal area, IVI) had higher explanatory power than did site conditions for understory species distributions. For understory flora, there was a decline in both species richness and diversity with a decrease in the canopy species. The variance in species richness, diversity, life-form, leaf-size spectrum and chorological affinities highlights the importance of canopy species of *Monotheca* dominated forests in maintaining understory species diversity and community stability in broadleaved evergreen forests. Our results also ease the understanding of understory species distributions in these stands.

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