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Elevation, aspect, and habitat heterogeneity determine plant diversity and compositional patterns in the Kashmir Himalaya

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Elevational gradient, slope, and aspect offer a unique opportunity to explore the response of plant species under changing environmental conditions. The present study aimed to analyze the species diversity and distribution patterns with respect to altitude, aspect, and habitat types in the Kashmir Himalayas. Considering major aspects and habitats, a total of 123 representative sites were selected along the elevational gradients for the present study. The plant species composition of each selected site was studied by organized sampling following the standard ecological methods. During the present study, a total of 361 vascular plant species belonging to 71 families and 214 genera were identified in the study area. At the lower altitudes, the southern aspect and drier habitats showed the highest diversity. Moreover, a significant amount of compositional dissimilarity was observed between the studied aspects, habitats, and elevation belts and was mainly due to species turnover rather than the nestedness component. Further, among the studied variables, altitude was the most important contributing variable, explaining the greatest variation in the species composition. The paired effects of altitude and habitat explained the maximum variation in plant species composition. It may be concluded that floristic diversity should be studied not only with reference to elevational gradients but should also include aspects and habitats. The current study will act as a reference in this direction. A similar study must be replicated in other parts of the Himalayan region in the future to improve our understanding of the distribution and preferences of plant species in mountainous zones. This, in turn, will be immensely helpful in the conservation and sustainable utilization of resources in these ecologically fragile regions.

KEYWORDS

Kashmir Himalaya, composition, β-diversity, variation partitioning, elevation

1. Introduction

In an ecosystem, the vegetational structure, composition, and function are among the significant attributes showing considerable variation with changing biotic and abiotic variables (Bisht and Bhat, 2013; Rawat et al., 2018; Wani et al., 2022a). Slope, aspect, elevation, and edaphic factors are some examples of the widely studied variables that shape the community structure and distribution of species, especially in mountainous ecosystems (Gairola et al., 2011;

Dar and Sundarapandian, 2016). Among these factors, the topographic factors significantly impact vegetation and plants' growth (Davies et al., 2007), especially when the research scale is narrow (Zhang et al., 2021). Therefore, it is imperative to undertake site-specific studies instead of regional and national ones to better understand the changing patterns of biodiversity and its key drivers, especially in mountainous regions. In mountainous regions, the topographic alterations are considerable, and local environmental conditions are complex. Topographic variations act as significant indicators because of their key role in influencing the temperature and moisture of the habitat (Raulings et al., 2010). The biotic and abiotic gradients on mountains have the enormous potential to improve our understanding of species distributions and richness patterns (McCain and Grytnes, 2010). The main biotic and abiotic factors under the local topographic influence are hydrology, incident solar radiation, wind exposure, geochemistry, and biotic conditions (Moeslund et al., 2013). Micro-climatic conditions may vary significantly over short spatial scales in mountainous areas due to the steep environmental gradients and thus substantially influence vegetation distribution and species richness patterns (McCain and Grytnes, 2010). Hamid et al. (2021) found significant differences in the edaphic properties along elevation gradients and changing aspects in their study. They also discovered that aspect play an important role, in addition to elevation, in determining the survival of plant populations in mountainous areas.

On a habitat scale, the presence of a species is limited by the vegetation structure, edaphic gradients, and management-related gradients of the habitat (Wamelink et al., 2014). These gradients within the habitats not only affect the overall vegetation composition but also substantially impact the distribution of native and alien plant species (Khuroo et al., 2011). According to previous studies (McCain and Colwell, 2011), altitudinal gradients in mountainous regions provide valuable natural settings for investigating the long-term ecological and evolutionary effects of environmental changes on different species. These gradients are characterized by several predictable changes in environmental factors, including a decline in temperature with increasing elevation and an average of $0.6°C$ per 100 m (Barry, 2008). Other abiotic factors that vary along the elevation gradients include decreasing air pressure and increasing solar radiation (Barry, 2008; McCain and Grytnes, 2010). However, precipitation does not change consistently with elevation on all mountains but varies greatly due to regional mountains and weather conditions (Barry, 2008). The gradients in these abiotic factors strongly influence the distribution of species along the elevation gradient. Owing to these changing abiotic factors with increasing elevations, it is believed that diversity decreases linearly with elevation (MacArthur, 1972; Korner, 1998); however, recent studies (Trigas et al., 2013; Zhou et al., 2018; Rawat et al., 2021) showed that plant diversity often peaks at mid-elevations (reflecting hump-shaped patterns of species richness), which vary among taxa and mountainous ranges in different climatic conditions across the world (McCain, 2007; Sharma et al., 2019). Therefore, altitude is one of the foremost ecological factors influencing the distribution of species and composition of the ecosystem and is thus significant for understanding the patterns of biodiversity in an ecosystem (Rezende et al., 2015).

The Himalayan mountains are among the highest in the world and act as treasure troves of biodiversity. The higher level of endemism in the region suggests the presence of diverse critical habitats and ecoregions of global importance in the region. Owing to the rich biodiversity of the region, it is among the world's major biodiversity hotspots (Khoshoo, 1992; Myer et al., 2000). The Himalayan mountains provide an altitudinal range representing the world's longest bioclimatic gradient (Grytnes and Vetaas, 2002). All these features have made the Himalayas an interesting candidate for biodiversity studies along the altitudinal gradients. Many researchers have studied patterns of species diversity along altitudinal gradients in the Himalayan region (Rawat et al., 2018; Ahmad et al., 2020; Bhat et al., 2020; Sharma and Kala, 2022). However, due to the remote and difficult-to-reach terrains in high-altitude areas, only a few studies have been conducted on the species composition and diversity in these remote areas of the Himalayas. As a result, the available information about vegetation distribution and its core drivers in the Himalayan mountains is scarce (Wani et al., 2022b). To address this knowledge gap, the present study attempts to examine plant species diversity and distribution patterns with respect to changing elevations, aspects, and habitat types in the Kashmir Himalaya—an integral part of the Himalayan Biodiversity Hotspot. The present study hypothesizes that species diversity and composition change with changes in elevation, aspect, and habitat types and that species diversity and richness decrease with an increase in elevation, with elevation being the most important factor determining changes in species diversity and composition.

2. Materials and methods

2.1. Study area

The Gulmarg Wildlife Sanctuary (GWLS) is located between $74°17'$-$74°79'$ N latitude and $34°55'$-$34°60'$ E longitude (Figure 1). The sanctuary is situated 52 km southwest of the Baramulla district, on the western side of Kashmir Himalaya within the Pir Panjal range. This sanctuary encompasses two administrative units: the Ferozpora/Tangmarg Block and the Gulmarg Block, covering a total area of 180 km^2. Furthermore, the sanctuary is composed of two distinct altitudinal regions, with 120 km^2 of the area falling in the alpine zone and the remaining 60 km^2 lying in the lower altitudinal area (www. jkwildlife.com, assessed on 15 April 2021). The natural beauty of Gulmarg and its proximity to Srinagar make it a popular destination for tourists, both local and international, attracting a huge influx of visitors annually (Nanda et al., 2019). The forest area of the sanctuary is primarily dominated by *Abies pindrow, Pinus wallichiana*, *Cedrus deodara*, *Picea smithiana,* and *Betula utilis*, with the latter forming the tree line in the region (Naqshi et al., 1984).

2.2. Site selection and data collection

Sites were selected randomly to represent each accessible aspect and habitat type along the vertical gradient. Physical characters and dominance of the vegetation were analyzed for habitat identification. The study classified habitats according to canopy cover, humus content, and moisture levels. Habitats with closed canopies and high levels of humus and moisture were referred to as "shady, moist habitats," while habitats with low levels of humus and moisture were referred to as "dry habitats." Habitats with high moisture

FIGURE 1
Location map of the study area.
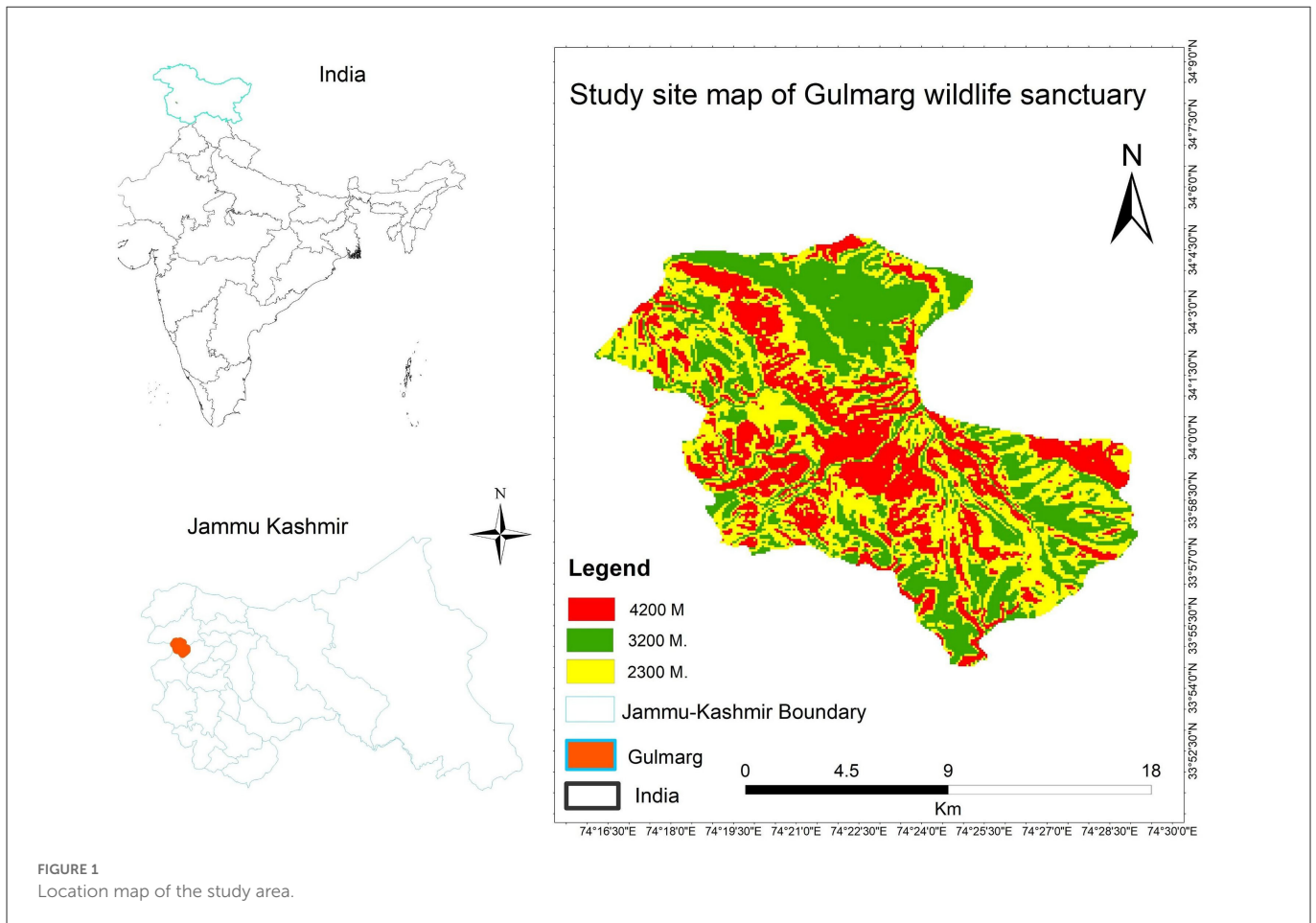
concentrations but no canopy cover were designated as "moist habitats." Habitats with more than 50% of their area covered by boulders were classified as "boundary habitats," and habitats with more than 50 rocks were classified as "rocky habitats." Grassland patches within forests were considered "open habitats." Additionally, habitats facing high levels of human-induced degradation, such as deforestation, overgrazing, and trampling, were classified as "degraded habitats." To assess the pattern of plant diversity in these habitats, vegetational sampling was conducted throughout the study area, taking into consideration environmental variables such as altitude, aspect, and habitat type. The plant species composition of each selected site was studied using the quadrat method, which is a widely-used and unbiased method of sampling (Bhatta et al., 2012). Elevation and aspect measurements were recorded using a Garmin GPS 73. The study area was mapped using ArcGIS 10.3. To assess diversity, plots of 50×50 m in the forest zone and 20×20 m in the alpine zone were established at each site. Within each plot, 10 (10×10 m) quadrats for trees, 10 (5×5 m) quadrats for shrubs, and 20 (1×1 m) quadrats for herbs were laid out at each elevational belt, representing different aspects and habitat types, following previous studies (Samant et al., 2007a; Negi et al., 2018; Rawat et al., 2018). As the alpine zone is devoid of trees, only 10 (5×5 m) quadrats for shrubs and 20 (1×1 m) quadrats for herbs were laid in each plot. Vascular plant species encountered during field surveys were collected, tagged, and brought to the laboratory, where they were mounted on

herbarium sheets using standard herbarium techniques (Smith, 1971; Jain and Rao, 1976; Smith and Chinnappa, 2015). All the collected specimens were identified to the species level using local floras (Bhat, 1984; Naqshi et al., 1984; Singh et al., 2002) and further authenticated at the Centre for Biodiversity and Taxonomy, University of Kashmir. The correct nomenclature and family were assigned to each identified plant species using the Plants of the World Online database[1].

2.3. Data analysis

Abundance data from all the sampling sites were analyzed in relation to aspect and habitat types. However, to study the diversity patterns along the altitudinal gradient, the total sampling sites were grouped into 20 100-m elevation belts, and the average species abundance at each 100-m elevational interval from 2,300 to 4,200 m above sea level was calculated. To estimate the total plant diversity at each site and each 100-m elevational belt, we used the Renyi diversity profiles within the vegan 2.5–7 package (Oksanen et al., 2020). The values of the Renyi diversity profiles ($H\alpha$) were calculated from the average abundance values of the quadrats laid out at each site and the elevational belt using a scaling parameter (α) ranging from zero to

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1 Powo (2022). Available online at: https://powo.science.kew.org.

infinity (Kindt and Coe, 2005) according to the following formula:

$$H_\alpha = 1 \frac{1}{1-\alpha} \ln \sum_{i=1}^{S} pi^\alpha,$$

where pi is the average abundance of a species at a site and α is the scaling parameter (Kindt and Coe, 2005; Oksanen et al., 2020). Diversity values were calculated for the default α scale of 0 to infinity following the study of Wani et al. (2022b). Further, a generalized additive model using the "mgcv" package was performed to analyze the impact of altitude on total species richness and the Shannon diversity index.

For analyzing the difference in the observed species composition among the selected sites and elevational belts, non-metric multidimensional scaling (NMDS) using abundance data was performed in a vegan 2.5-7 package (Oksanen et al., 2020). According to the NMDS, the studied sites are ordered in a multidimensional space so that the sites with comparable floristic compositions are assembled in the ordination diagram (Hochstedler et al., 2007; Rawat et al., 2021). Further, to evaluate its accuracy, the associated stress value was calculated. The value of associated stress ranges from 0 to 1; 0 represents no stress, whereas 1 represents a complete lack of fit (Legendre and Legendre, 2012; Rawat et al., 2021; Shahabuddin et al., 2021). The observed degree of compositional dissimilarities between the selected sites was statistically tested using the permutational analysis of variance (PERMANOVA), wherein both the Bray–Curtis and Jaccard indices were used to investigate whether species relative abundances or the presence and/or absence of species are responsible for the observed compositional differences (Shahabuddin et al., 2021). The associated statistical significance was calculated by setting alpha at 0.05 based on 999 permutations.

Moreover, the overall and pairwise β diversity between the studied sites and elevational belts was calculated using the beta version 1.5.4 package (Baselga et al., 2021). This method uses presence/absence data and separates the observed dissimilarity (β_{SOR}) into species turnover (β_{SIM}) and nestedness (β_{SNE}) (Baselga and Orme, 2012). It also clusters different aspects and habitat types along elevation belt-based dissimilarity resulting from both β_{SIM} and β_{SNE} components separately. Additionally, variation partitioning was performed to investigate the relative effects of altitude, aspect, and habitat type on plant species composition using the varpart function from the vegan package version 2.5-7 (Oksanen et al., 2020). This method partitions the total variation into seven fractions attributed to (i) the individual effect of altitude (A), (ii) the individual effect of aspect (AS), (iii) the individual effect of habitat (H), and the shared effect due to each possible pair (iv) altitude and aspect (A n AS), (v) altitude and habitat (A n H), (vi) aspect and habitat (AS n H) and the combined effect of all three underlying variables, and (vii) altitude, aspect, and habitat (A n AS n H). We evaluated the associated statistical significance based on the Monte Carlo permutation test using 999 permutations. As the shared effects were obtained simply by subtraction, they were not tested for statistical significance (Legendre and Legendre, 2012).

3. Results

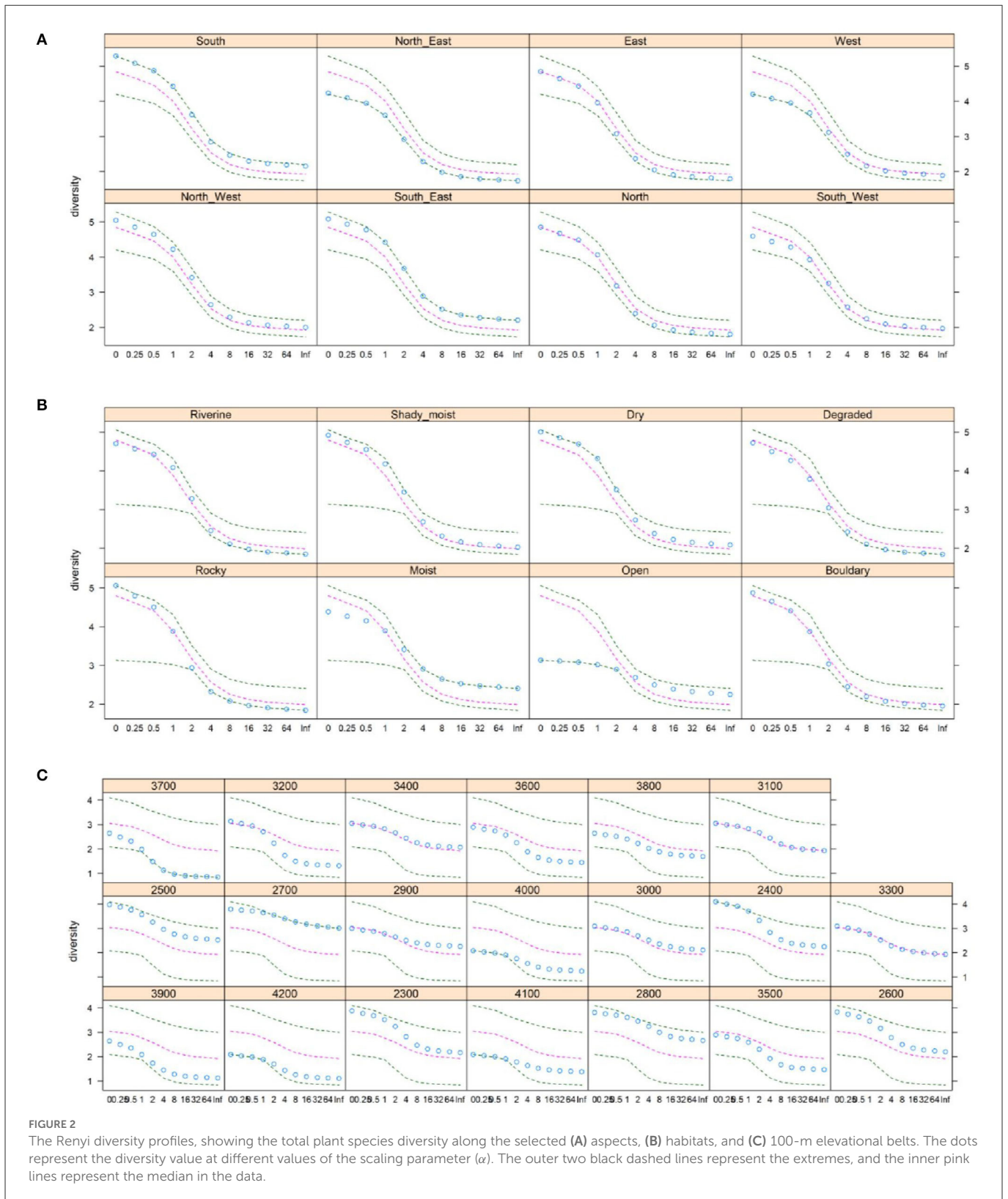In the present study, a total of 123 sites were sampled, representing all possible aspects and habitat types in the study area. Of these sites, the greatest number (25) were in the southern aspect, followed by the northern (20), northwest (19), eastern (17), southeast (13), northeast (11), southwest (10), and western (8) aspects. The habitats of the sites were primarily represented by shady moist at 27 sites, followed by rocky (24), bouldary (20), degraded (17), riverine (13), dry (12), open (6), and moist (4). A total of 361 plant species from 71 families and 214 genera were identified from the study area (Supplementary Table S1). The *Asteraceae* were the dominant family with 54 species, followed by the *Lamiaceae*, *Rosaceae*, and *Ranunculaceae* with 23, 20, and 19 species, respectively. The *Ranunculus* genus was the most prevalent with seven species, followed by *Anaphalis* and *Nepeta* with six and five species, respectively. The dominant growth form was represented by herbaceous forms (82.7%), followed by shrubs (10.5%), trees (5.7%), and climbers (1.1%).

3.1. Diversity patterns

The Renyi diversity profiles for the selected aspects are presented in Figure 2A. The diversity profile revealed that the highest plant species diversity was found in the southern aspect at the scaling parameter (α) values between 0 and 1, while the diversity was higher in the southeast aspect for the rest of the scaling parameter (α) values. In contrast, the lowest plant species diversity was observed at the northeast aspect at all scaling parameter (α) values (Figure 2A). Furthermore, the Renyi diversity profiles for the studied habitat types are presented in Figure 2B. The highest plant species diversity was observed in dry habitats at α values between 0 and 2 and in moist habitats for the remaining scaling parameters. In contrast, the lowest plant species diversity was found in open aspects at α values between 0 and 2 but in rocky and degraded habitats for the remaining α values (Figure 2B). Additionally, the Renyi diversity profiles for the selected elevation belts showed that the highest plant species diversity was found at an elevation of 2,400 m for α values between 0 and 1 but at a 2,700-m elevation belt for the remaining α values. In contrast, the lowest species diversity was found at an elevation of 4,200 m for α values between 0 and 1 but at 3,700 m for the remaining α values (Figure 2C). Furthermore, GAM analysis revealed that total species richness and diversity decreased with an increase in elevation and follow a unimodal pattern (Figure 3).

3.2. Plant species composition

The NMDS analysis revealed greater compositional dissimilarity among the selected aspects. More precisely, a varying degree of overlap was observed between the southwest (SW), northwest (NW), and south (S) aspects. The west (W) aspect was the most dissimilar in terms of plant species composition from the rest of the aspects. However, the partially overlapping ellipses indicate that the composition of the plant species in other aspects was not as significantly different (Figure 4). Moreover, the associated stress level for the NMDS plot was very low (0.10) for the first three dimensions. The PERMANOVA analysis indicated significant compositional differences among the studied aspects due to both changes in the number and relative abundance of species (Jaccard: $F = 31.88$, $p < 0.001$; Bray-Curtis: $F = 25.20$; $p < 0.001$).

FIGURE 2
The Renyi diversity profiles, showing the total plant species diversity along the selected **(A)** aspects, **(B)** habitats, and **(C)** 100-m elevational belts. The dots represent the diversity value at different values of the scaling parameter (α). The outer two black dashed lines represent the extremes, and the inner pink lines represent the median in the data.

Based on the studied habitat types, the NMDS analysis revealed a significant extent of compositional differences among the studied habitats (Figure 5). The open habitats were the most dissimilar in terms of plant species composition from the rest of the studied habitats. Moreover, the associated stress level for the NMDS plot was very low (0.13) for the first three dimensions. The PERMANOVA analysis indicated significant compositional differences among the studied habitats due to both changes in the number and relative abundance of species (Jaccard: $F = 43.14$, $p < 0.001$; Bray–Curtis: $F = 36.01$; $p < 0.001$).
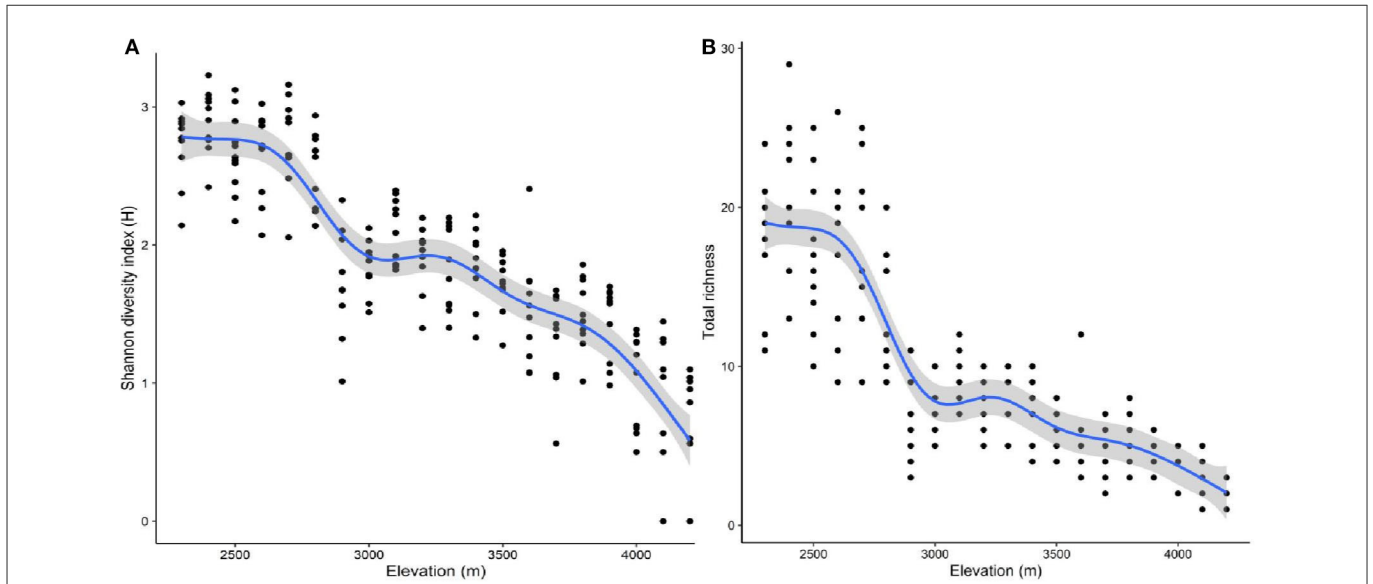
FIGURE 3
The relationship between elevation and **(A)** the Shannon diversity index and **(B)** total species richness. *The blue lines represent the best-fit regression splines from GAM; the gray shading represents the standard errors; and the black dots represent the observations.
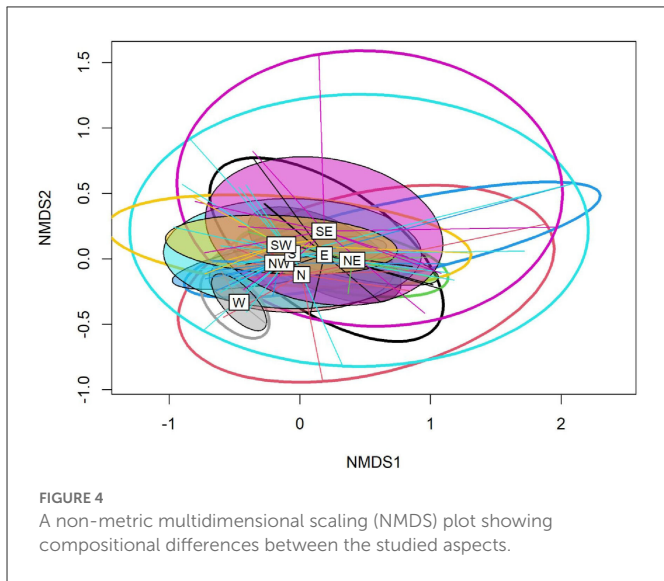

FIGURE 4
A non-metric multidimensional scaling (NMDS) plot showing compositional differences between the studied aspects.
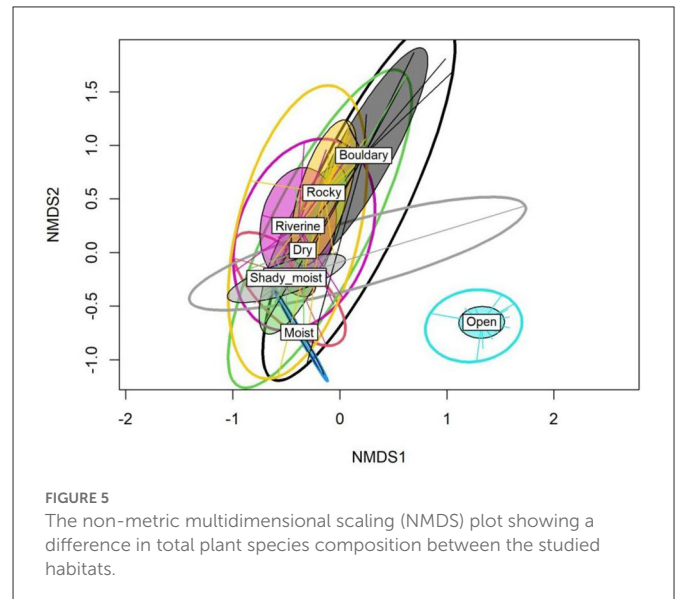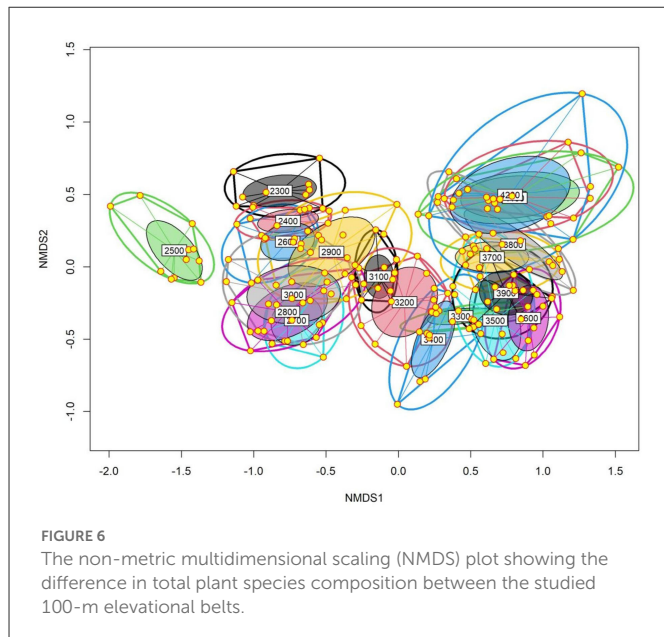

FIGURE 5
The non-metric multidimensional scaling (NMDS) plot showing a difference in total plant species composition between the studied habitats.

Based on altitude, the results of the NMDS analysis revealed a significant extent of dissimilarity in the total plant species composition between the studied elevation belts (Figure 6). A significant degree of overlap was observed between the sites at lower altitudes, except for those at 2,500-m above the sea level, and the sites at higher altitudes, representing the forest and alpine communities, respectively. Additionally, the cluster formed by the lower elevational belts is connected to the higher elevational cluster by four elevation belts, e.g., 3,100–3,400 m, representing the ecotone. Similar to aspect and habitat types, the associated stress level for the NMDS plot was very low (0.11) for the first three dimensions. The PERMANOVA analysis indicated a significant compositional difference among the altitudinal belts due to both changes in the number and relative abundance of species (Jaccard: $F = 17.63$, $p < 0.001$; Bray–Curtis: $F = 29.69$; $p < 0.001$).

3.3. Spatial β-diversity patterns

Overall, the observed multiple-site Sorensen dissimilarity index among the selected aspects was high ($\beta_{SOR} = 0.71$). The contribution of species turnover to the observed dissimilarity was relatively much higher ($\beta_{SIM} = 0.57$) than the nestedness component ($\beta_{SNE} = 0.13$). Furthermore, a significant variation was observed for the pairwise Sorensen dissimilarity index, with the highest β_{SOR} found between the west and southeast aspects ($\beta_{SOR} = 0.70$). The contribution of β_{SIM} to the resulting pairwise dissimilarity was greater than that of the βSNE component in most comparisons (Supplementary Table S2). This suggests that the observed dissimilarity was greater due to β_{SIM} than the β_{SNE} component (Figure 7A). A cluster analysis based on the β_{SIM} component revealed the southwest aspect was significantly

FIGURE 6
The non-metric multidimensional scaling (NMDS) plot showing the difference in total plant species composition between the studied 100-m elevational belts.

different from the rest of the selected aspects in terms of species composition, followed by the southeast and east aspects (Figure 7B). In contrast, a cluster analysis approach based on the β_{SNE} component indicated that the south aspect was highly dissimilar in terms of species composition from the rest of the selected aspects (Figure 7C).

An analysis of habitat types revealed a high multiple-site Sorensen dissimilarity index ($\beta_{SOR} = 0.75$). The contribution of the turnover component to this dissimilarity was higher ($\beta_{SIM} = 0.64$) than that of the nestedness component ($\beta_{SNE} = 0.10$). Further, a significant difference was also observed for the pairwise Sorensen dissimilarity index, with the highest β_{SOR} found between the open and riverine habitats ($\beta_{SOR} = 0.84$). The contribution of β_{SIM} to the resulting pairwise dissimilarity was greater than that of the β_{SNE} component (Supplementary Table S2). This suggests that the observed dissimilarity was primarily due to the β_{SIM} component rather than the β_{SNE} component (Figure 8A). A cluster analysis based on the β_{SIM} component identified the moist habitat as being highly different from the rest of the other selected habitats in terms of plant species composition, followed by bouldary and riverine habitats (Figure 8B). In contrast, a cluster analysis approach based on the β_{SNE} component indicated that open habitats have a highly distinct plant species composition compared to the other studied habitats (Figure 8C).

The analysis of the selected elevational belts revealed a much higher multiple-site Sorensen dissimilarity index ($\beta_{SOR} = 0.92$), with a greater contribution from species turnover ($\beta_{SIM} = 0.88$) than from nestedness ($\beta_{SNE} = 0.04$). Further, a significant difference was observed for the pairwise Sorensen dissimilarity index, and once again, the contribution of β_{SIM} to this pairwise dissimilarity was greater than that of the β_{SNE} component (Supplementary Table S2). This indicates that the observed dissimilarity was primarily due to β_{SIM} than the β_{SNE} component (Figure 9A). A cluster analysis based on the β_{SIM} component resulted in four major clusters, representing lower, higher, sub-alpine elevational belts (ecotones), and a distinct cluster at 2,500-m altitude (Figure 9B). In contrast, a cluster analysis approach based on the β_{SNE} component resulted

in three clusters representing lower, higher, and extreme higher elevation belts (Figure 9C).
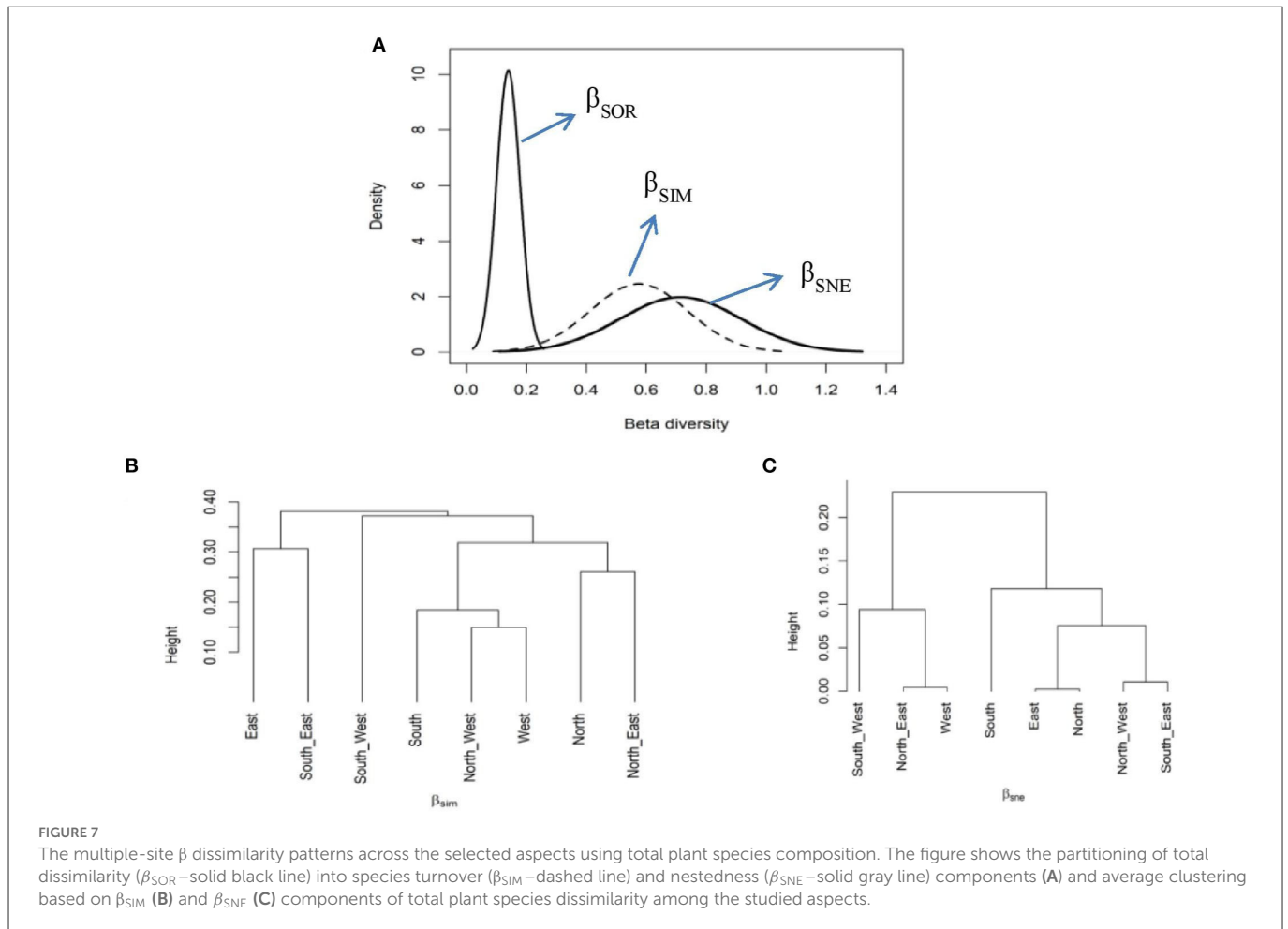
3.4. Variation partitioning

In terms of variation partitioning, the results for plant species composition showed that the total variation explained by the three variables (altitude, aspect, and habitat) was 16.5% (Figure 10). Of the individual effects, altitude (A) turned out to be the most important contributing variable, explaining the greatest amount of variation (9.7%) in plant species composition (Table 1). In addition, the individual effects of aspect (AS) and habitat type (H) were relatively small at 3.4 and 9.4%, respectively (Figure 10; Table 1). Furthermore, the variation explained by each variable was statistically significant (Table 1). Notably, the paired effect of altitude and habitat (A n H) explained the maximum variation (14.2%) in plant species composition.

4. Discussions

Topographic and environmental conditions in the Himalayan region vary significantly, leading to variations in biodiversity patterns with respect to aspect, elevation, and habitat types (Rana et al., 2020; Ahmad et al., 2021). Many workers in the Himalayan region have studied the effects of topography on plant species diversity and composition (Vetaas and Grytnes, 2002; Carpenter, 2005; Kharkwal et al., 2005; Paudel and Vetaas, 2014; Subedi et al., 2020; Rawat and Negi, 2021; Wani S. A. et al., 2022). These studies have revealed that species diversity and composition vary significantly with changes in the topographic features of a region. The Gulmarg Wildlife Sanctuary (GWLS) embodies a broad elevation range with complex topography, providing a large variation in environmental variables to harbor higher species richness in a smaller area. The species richness reported in the present study was comparatively higher (361 species) than earlier reports from the Indian Himalayan region, i.e., Chawla et al., 2008 (313 species), Haq et al., 2018 (183 species), Ahmad et al., 2020 (255 species), and Haq et al., 2021 (181 species). The higher species richness recorded in the present study may be attributed to the fact that the present study was extensive and covered forest and alpine zones of the study area. *Asteraceae*, *Lamiaceae*, and *Ranunculaceae* were the most dominant families in the study area; these families have also been reported as being dominant in the Himalayan region (Dar and Khuroo, 2013; Ahmad et al., 2021; Altaf et al., 2021). These plant families have larger ecological amplitudes and wide distributions, increasing the possibility of encountering the members of these families (Mumshad et al., 2021). The dominance of herbaceous growth forms in the present study is in accordance with several other studies conducted in the Indian Himalayan region (Samant et al., 2007b; Malik et al., 2015; Sharma et al., 2019; Haq et al., 2021; Rawat et al., 2021). It may be due to the fact that herbs are considered common growth forms in most mountainous regions owing to their ability to acclimate to an extensive range of ecological settings (Wani S. A. et al., 2022).

In the present study, we calculated the plant species diversity more robustly than the randomly chosen single diversity index method, which led to biased generalizations and outcomes (Ahmad et al., 2019). The present study revealed that southern and southeast

FIGURE 7
The multiple-site β dissimilarity patterns across the selected aspects using total plant species composition. The figure shows the partitioning of total dissimilarity (β_{SOR} −solid black line) into species turnover (β_{SIM} −dashed line) and nestedness (β_{SNE} −solid gray line) components **(A)** and average clustering based on β_{SIM} **(B)** and β_{SNE} **(C)** components of total plant species dissimilarity among the studied aspects.
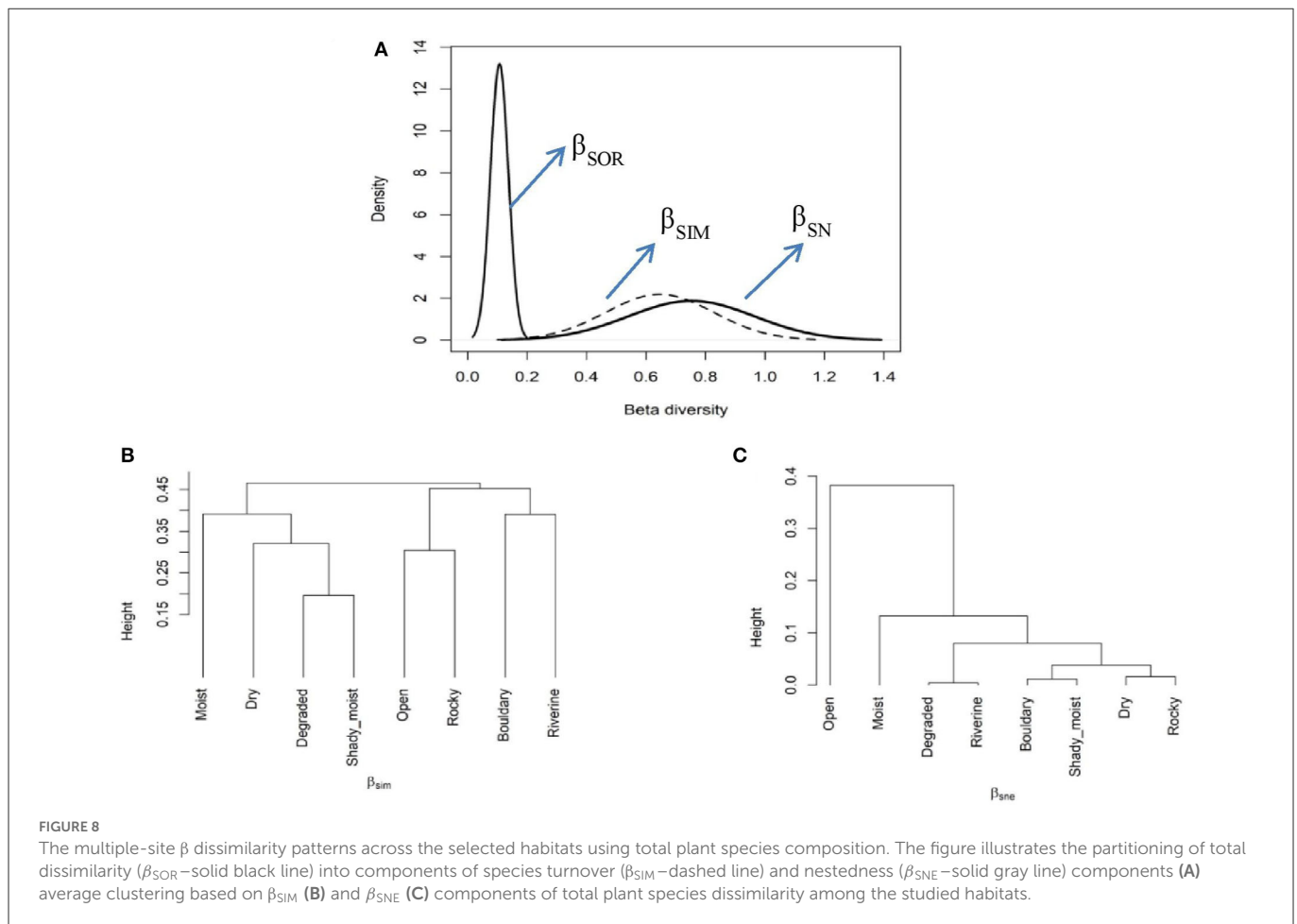
aspects favor rich plant species diversity, which is in accordance with the findings of previous studies (Winkler et al., 2016). This pattern may be attributed to the differential degree of exposure to sunlight and, thus, temperature differences with respect to changing aspects (Korner and Hiltbrunner, 2018). Aspect causes prominent temperature alterations and therefore affects species richness and composition in the mountains indirectly by affecting the soil-plant-atmosphere continuum (SPAC) (Aalto et al., 2013). The south aspect receives higher inputs of solar radiation in comparison to the north and west-facing aspects (Nepali et al., 2021). Furthermore, in temperate mountain regions like the study area, convective cloud formation is a common phenomenon (Geiger, 1950). This results in reduced daily solar radiation on the western aspect compared to the southern aspect.

Temperature is the most significant abiotic factor affecting plant growth and physiology at higher elevations (Korner and Hiltbrunner, 2018). Aspect causes prominent alterations in the thermal input and thus considerably affects the biodiversity on a mountain slope (Hamid et al., 2020). Further, the heterogeneity in aspect and altitude within a landform shows an important correlation with habitat heterogeneity (Aguilar-Santelises and del Castillo, 2013). During the present study, it was found that certain species, such as *Oxyria digyna, Nasturtium officinale, Rorippa islandica, Caltha alba, Ranunculus trichophyllus,* and *Polygonum amphibia,* prefer riverine habitats, whereas species such as *Valeriana jatamansii, Viola odorata, Silene*

baccifera, Epimedium elatum, and *Ainsliaea Aptera* prefer shady, moist habitats. These species, which have narrow habitat preferences and specialized ecological niches, are less tolerant and less resilient, making them more susceptible to extinction (Wani S. A. et al., 2022; Wani et al., 2022c) compared to those species with wider habitat preferences.

Further, open and degraded sites were populated with exotic species such as *Rumex* sp., *Digitalis grandiflora, Sambucus wightiana, Leucanthemum vulgare,* and *Achillea millifolium.* Thus, due to habitat destruction, plant species with specific habitat preferences may suffer, and the whole community structure may be altered due to the increasing invasion of alien species (Fletcher et al., 2018; Fahrig et al., 2019). Habitats not only play an imperative role in the growth and development of species but also maintain species diversity. Habitat fragmentation and degradation are considered the primary causes of biodiversity loss (Su et al., 2022). As such, the preservation of habitats is equally important to the conservation of particular species.

The plant species diversity and richness decreased with increasing altitude due to environmental filtering and the dominance of plant species tolerant of extreme environmental conditions at higher altitudes (Trigas et al., 2013; Rana et al., 2020). According to the climate hypotheses, if the temperature is the main determinant of elevational species richness, the pattern predicted is decreasing diversity with increasing elevation (Heaney, 2001; McCain, 2007). The disparity in species composition and richness with changing

FIGURE 8
The multiple-site β dissimilarity patterns across the selected habitats using total plant species composition. The figure illustrates the partitioning of total dissimilarity (β_{SOR}−solid black line) into components of species turnover (β_{SIM}−dashed line) and nestedness (β_{SNE}−solid gray line) components **(A)** average clustering based on β_{SIM} **(B)** and β_{SNE} **(C)** components of total plant species dissimilarity among the studied habitats.

altitude is a common phenomenon in the Himalayan and other mountainous ecosystems across the globe (Khuroo et al., 2011; Rawat et al., 2018). In the present study, species composition at lower altitudes was different than at higher altitudes. Mid-altitudes (3,100 and 3,400m) representing the ecotone form a transition between the lower and higher altitudes and are occupied by species from both lower and higher altitudes, forming a distinct cluster in terms of species composition.

Further, the 2,500-m elevation belt was found to be dissimilar from the rest of the lower altitudinal belts. The possible reason for this can be the observed anthropogenic pressure owing to the nomadic (Gujjars and Bakerwals) settlements at particular elevational belts. In the present study, total plant species richness and diversity followed a unimodal pattern, which is considered a general pattern (Stevens, 1992). However, analysis of wide-ranging elevational gradients usually results in hump-shaped patterns, while the exclusion of elevations of the gradient at the higher or lower ends favors a monotonic upsurge or decline with elevation (Fontana et al., 2020). At higher altitudes, plant species are exposed to various eco-physiological limitations, which in turn reduce species richness and diversity (Ahmad et al., 2020). In contrast, the higher species richness and diversity at lower and mid-elevations are chiefly associated with favorable environmental settings (Manish, 2021).

β-diversity, a central element of species diversity, provides insights into the extent to which environmental heterogeneity is partitioned by different species (Rawat et al., 2003). Greater

β-diversity values indicate a higher level of species variation in response to environmental gradients (Bisht and Bhat, 2013). In the present study, we found relatively higher plant species diversity in southern aspects and dry habitats, likely due to the prominence of heliophytes and early successional species in forest gaps (Li et al., 2019). The patterns of β-diversity may be associated with the degree of variation in habitats along altitudinal gradients and changing aspects (Tang and Fang, 2004). Comparing compositional dissimilarities among the studied sites, further partitioned into species replacement and nestedness as attempted in this study, allows a better understanding of how biodiversity is assembled across environmental variables. Both these components of β-diversity have been acknowledged to sufficiently perceive spatial diversity patterns due to the underlying dissimilarity measures which compare species composition between two sampling units. Species replacement is supposed to be driven by environmental influences, while nestedness may reflect extinction patterns (Fontana et al., 2020). The present study revealed that turnover was more prominent than nestedness for all the studied variables (aspect, habitat, and elevation), which is consistent with the idea that the environmental filtering effects on vegetation structure along environmental gradients primarily result in turnover (Anderson et al., 2011; Zellweger et al., 2017). Furthermore, we found that the values of turnover and total β-diversity were more prominent along the elevational gradient than variation in aspects and habitat types. Temperature and solar radiations are the most important variables that influence β-diversity

FIGURE 9
The multiple-site β dissimilarity patterns for the selected elevation belts using total plant species composition. The partitioning of total dissimilarity (β_{SOR}−solid black line) into components of species turnover or replacement (β_{SIM}−dashed line) and nestedness (β_{SNE}−solid gray line) components **(A)** is shown. This figure represents the average clustering based on β_{SIM} **(B)** and β_{SNE} **(C)** components of total plant species dissimilarity among the studied elevational belts.

FIGURE 10
The variation in total plant species composition explained by altitude, aspect, and habitat types, as indicated by the adjusted R^2 values.
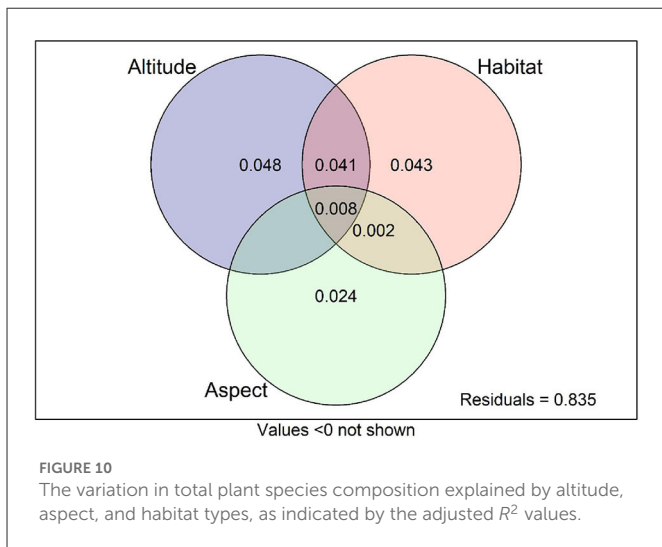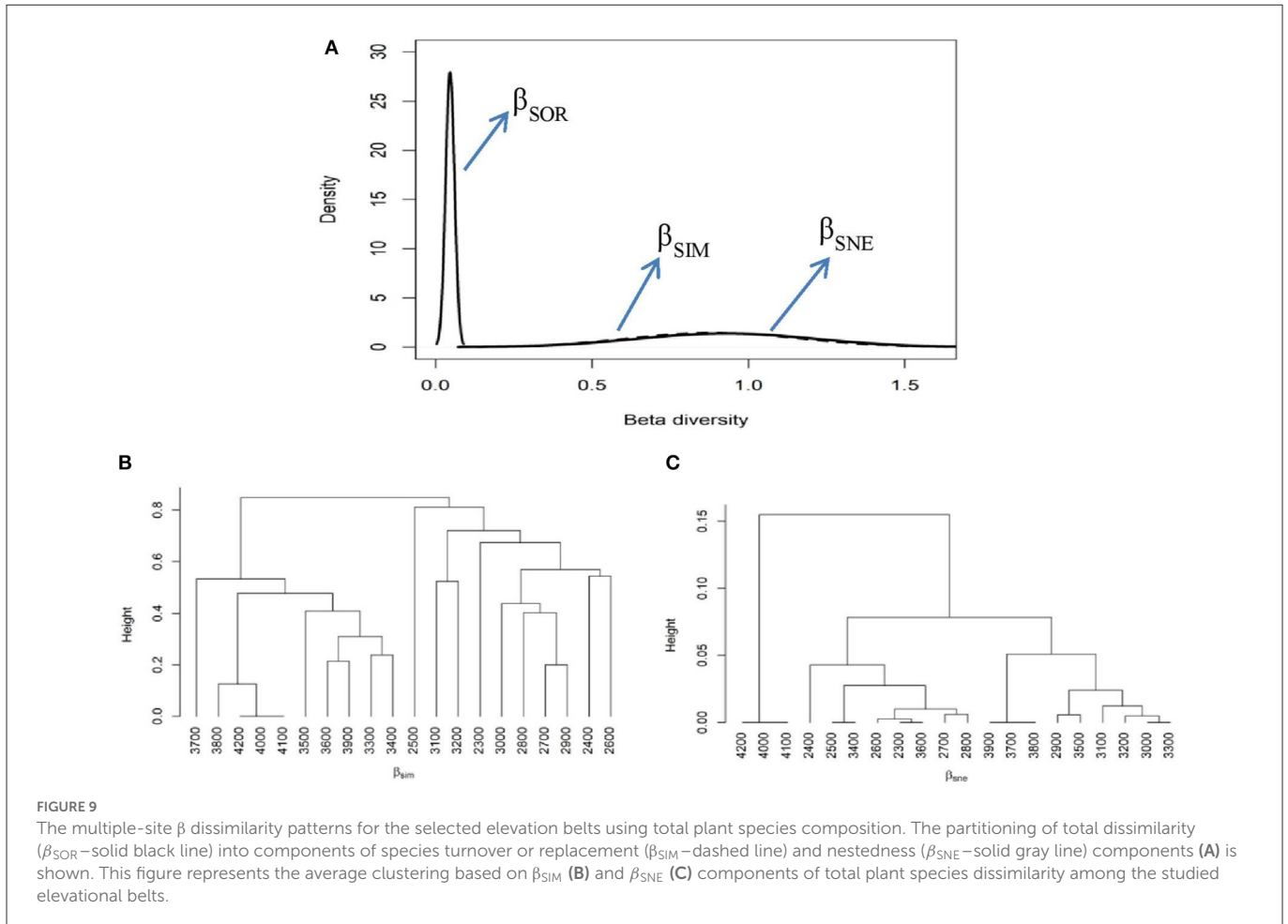
TABLE 1 A variation partitioning analysis, displaying the individual and combined effects of altitude (A), aspect (AS), and habitat type (H) on plant species composition.

	Individual effect			Combined effect			
	A	AS	H	A∩AS	A∩H	AS∩H	A∩AS∩H
Composition	9.7 (0.001)	3.4 (0.001)	9.4 (0.001)	12.3	14.2	11.8	16.5 (0.001)

The values presented are the adjusted R-squared values as a percentage, with corresponding p-values based on 999 permutations in brackets.
The values indicate the adjusted R^2 values in percentage along with the p-values based on 999 permutations in brackets.

present study, variation in altitude was found to be the main factor leading to variation among the studied sites. Rawat and Negi (2021) also found that elevation is the most influential variable influencing species distribution patterns. The combined effect of altitude and habitat on species composition and richness among the sites was also found to be significant. Environmental and resource parameters determine the growth and competitive interactions of species, while environmental heterogeneity parameters tend to enhance coexistence and favor higher species richness. It is crucial to consider both levels of environmental parameters and heterogeneity concurrently to distinguish between the two types of parameters. Environmental heterogeneity is scale dependent and may create high niche diversity, allowing species to coexist at a large spatial scale.

along an elevational gradient. Additionally, a significant percentage of plant species (specialists) is restricted to certain ecological zones and does not colonize entire environmental gradients (Broennimann et al., 2006; Trigas et al., 2013).

Environmental and topographic variables are significant factors in the distribution of plant species within an ecosystem. In the

5. Conclusions

The present study revealed that elevation is the most important factor contributing to variations in plant species diversity and composition. However, the present study also highlighted the importance of aspect and habitat heterogeneity in determining plant species richness. The southern aspect was found to support higher plant diversity compared to other studied aspects due to its greater exposure to sunlight. Furthermore, the plant species found in the study region exhibit distinct ecological preferences. For example, *Betula utilis* is found along northern aspects.

Similarly, the recorded species have varying habitat preferences. Therefore, the present study suggests that floristic diversity should be studied not only in relation to elevational gradients but also in relation to aspects and habitats. This study serves as a model for future research in this direction. Similar studies should be conducted in other parts of the Himalayan region to expand our understanding of the distribution and preferences of plant species in mountainous areas. This, in turn, will greatly aid in the conservation and sustainable utilization of resources in these ecologically fragile regions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

ZW: conceptualization, methodology, data collection, curation and analysis, investigation, and writing an original draft. VN and JB: writing—review and validation. KS, SK, RD, and RA-Q: writing—review. AK: prepared the map of the study area and writing—review. SS: writing—review and funding acquisition. SP: conceptualization, methodology, supervision, validation, and writing—review. All authors contributed to the article and approved the submitted version.

Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1019277/full#supplementary-material

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