Chapter 4
Ecological Determinants of Woody Plant Species Richness in the Indian Himalayan Forest

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Abstract The ecological importance of woody plant species richness is well known. The role of abiotic ecological determinants on structuring the vegetation has been well studied. The present study evaluated the independent and integrated strength of the abiotic and biotic determinants in explaining species richness of woody plants in the Indian Himalayan forest. The primary field inventory data was collected using nested quadrat method (tree species at 10 × 10 m^2, shrub species at 5 × 5 m^2, and herb species at 1 × 1 m^2 quadrats) for different life forms and for the abundance estimation within each 1 km transect. Each transect was laid in a 6.3 × 6.3 km^2 grid on the study site. The biotic determinants included diameter at breast height (d.b.h.) and tree height, whereas the abiotic determinants were temperature, precipitation, soil moisture, relative humidity and elevation. A total of 302 woody plant species (233 genera and 53 families) were recorded from the field inventory. The woody plant species richness was found to range from 1 to 54 per ha at transect level. Structural Equation Model (SEM) evaluated different combinations of ecological determinants for woody plant species richness. The abiotic or biotic determinants were non-significant if considered independently; however, the integration of both resulted in a significant relation with woody plant species richness. The best combination of ecological determinants include density d.b.h. ≥ 2.5 cm, tree height, relative humidity, and elevation ($R^2 = 0.53$). Overall, the integration of biotic and abiotic determinants better explained woody plant species richness in the Indian Himalayan forest.

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4.1 Introduction

Ecological variability (biodiversity and environmental heterogeneity) is an important indicator of ecosystem function and ecosystem health (Gaston and Spicer 2013). In particular, understanding the dynamics of species diversity is an important aspect of many habitats. As the absolute number of species can change over time, due to climatic variability, speciation, extinction, or dispersal events and rapid land-use change, the persistence of predictable patterns tell us that such events and their consequences are somehow geographically constrained (Groom et al. 2006; Latham and Ricklefs 1993; Mahanand and Behera 2019). Therefore, factors governing species compositions, structure, and patterns are of primary interest to ecologists.

Woody plant species are usually characterized by trees and shrubs with the diameter at breast height (d.b.h.) of ≥1 cm (Condit 1995), ≥2.5 cm (Gentry 1982) and ≥10 cm (Gentry 1988; Smith et al. 1998). Canopy patches beneath woody plants and the inter canopy patches experience heterogeneous patterns of energy, water, and biogeochemistry, and the level of this heterogeneity depends on the architecture of woody plant canopies (Breshears 2006; Pandey et al. 2018). Thus, the higher richness of woody plant species in a habitat effectively maintains the microenvironment in terms of reduced soil erosion and air temperatures, wind speed and radiation (Blondel et al. 2010; Pickett et al. 2009). Consequently, it enhances the soil moisture content and relative humidity (Fine 2015). Alternately, increased radiation is often associated with reduced water availability, resulting in low woody plant species richness (Pausas and Austin 2001; Vereecken et al. 2015). The relationship of plant species richness to abiotic determinants often account for >80% of the spatial variation in richness; however, there is no global consistency due to scale variant characters (Asner et al. 2017; Francis and Currie 2003; Li et al. 2019).

Several complex and interacting abiotic determinants such as topography (Körner 2004), edaphic factors (Hawkins et al. 2003; Russell-Smith 1991), precipitation (Hawkins et al. 2006), soil moisture (van der Molen et al. 2011), natural disturbances (Sinha et al. 2018), and anthropogenic disturbances (Gogoi and Sahoo 2018; Lakshminarasimhan and Paul 2018) have been identified as predictors of woody-plant species richness in tropical forests. Moreover, the optimized range of these interacting abiotic determinants (temperature, radiation, soil moisture) supports higher woody plant species richness (Blondel et al. 2010; O'Brien 1998). Many of these predictors of species richness are region-specific due to the unique evolutionary, geographic, and land-use histories of each region (Pennington et al. 2009; Whittaker et al. 2001). The Indian Himalayan forest is the part of a global biodiversity hotspot and encompasses a large fraction of global climate and plant diversity as well (Bookhagen and Burbank 2010; Fick and Hijmans 2017). The major forest types observed are tropical moist deciduous forests along the foothills of the Himalaya, while the temperate broad-leaved forests are found between 1500 and 3000 m elevation in the eastern Himalaya. Moreover, the region also harbors broad-leaved hill forests, subtropical forests, temperate mixed forests and wet/dry evergreen forest (Roy et al. 2015). In a phytogeographical sense, forests of this region are species rich, and harbor a number of phylogenetically primitive plant species and hence regarded as a “treasure trove” of ancient and unique vegetation (Champion and Seth 1968). However, climatic variability has clearly affected plant speciation, extinction, and dispersal events in the Himalaya (Manish and Pandit 2019). All these issues need to be addressed in order to protect and conserve the unique biodiversity of the Indian Himalayan forest (Banerjee et al. 2019; Basnett et al. 2019; Mehta et al. 2020).

The abiotic determinant, namely temperature was found to be a limiting factor for the woody plant species richness in the temperate forests (Currie 1991), whereas studies in tropical regions emphasize the importance of moisture and related factors (Brown 1990). Moreover, a study in the subtropical region compared different abiotic determinants and found that relative air humidity and soil moisture significantly explained the plant species richness (Drissen et al. 2019). A study in east Nepal confirmed the significance of precipitation and moisture in explaining woody plant species richness (Bhattarai and Vetaas 2003). Although, species richness and distribution patterns of plants are largely regulated by elevation and other environmental factors (Saikia et al. 2017), it has been pointed out that many components of climate and local environment (e.g., temperature, precipitation, seasonality and disturbance regime) vary along the elevation gradients and ultimately create the variation in species richness (Lomolino 2001). The declining trend of species richness along elevation gradient has been recently reported for the Indian Himalayan forests (Bhutia et al. 2019; Malhi et al. 2010). Studies focused on deforestation and land use effect along the elevational range of Sikkim Himalaya, summarised that the primary forests at higher elevational range are subject to low deforestation compared to the broadleaf forest ranging from low to higher elevational range (Kanade and John 2018).

The biotic determinants have been identified or documented based on qualitative assessment in the Indian Himalayan forest (Chatterjee et al. 2006; Singh and Sanjappa 2011; Tambe and Rawat 2010). For Sikkim Himalaya, the different plant structural components (tree species richness, density d.b.h., basal area and distribution range) were evaluated along with the elevational range and summarized as highest tree density and richness at 1000 m elevation of Sikkim (Pandey et al. 2018). Shooner et al. (2018), report an inverse relationship between elevation and species richness along an elevation gradient in Arunachal Pradesh. Sharma et al. (2019), in Sikkim Himalayas, report a hump shaped richness pattern along elevation gradient. Other explorations utilized the phenological traits of woody species and found significance for the abiotic determinants (day length and temperature), while the role of elevation was not significant in Sikkim Himalaya (Basnett et al. 2019; Ranjitkar et al. 2013). Bhutia et al. (2019) report an inverse ‘J’ shaped species richness emphasizing the role of abiotic determinants and habitat filtering to explain this pattern.

The distribution of species is partly determined by ecological gradients of water, nutrients, heat and radiation, and partly by biotic determinants, stochastic events or disturbances caused by natural events or forest management (Austin and Smith 1990). Pau et al. (2012), analysed the influence of abiotic and biotic factors in determining woody plant species richness and productivity, and concluded the direct effect of precipitation (0.72) and its mediation through plant structure (0.74), in the dry forests of Hawaii island. However, there are studies that have only evaluated either abiotic or biotic determinants to understand the woody plant species richness in Indian Himalayan forest and hardly any work have considered both these factors together (Dutta and Devi 2013; Gogoi and Sahoo 2018; Sinha et al. 2018). Therefore, it is essential to consider both abiotic and biotic determinants together to reach a better understanding of the composition of woody plants in the Indian Himalayan forest.

This is a maiden attempt to evaluate the independent as well as integrated effect of ecological determinants (i.e., biotic and abiotic) to explain the richness of woody plant species in the Indian Himalayan forest. The geography greatly challenges the relationship between woody plant species richness and abiotic determinants and yet to be generalized. On the other hand, woody plant structure plays an important role to modify the microenvironment. The present study aimed to explore (i) the significance of a best individual ecological determinant, and (ii) the best combinations of ecological determinants to explain the woody plant species richness in Indian Himalayan forest.

4.2 Methods

4.2.1 Study Area

We selected the following states and respective districts in India for this study that run along the foothills of Himalaya, i.e., Assam (Dhubri, Kokrajhar, Bongaigaon, Barpeta, Goalpara, Nalbari), Sikkim (East, West, North, South), and West Bengal (Malda, Uttar Dinajpur, Dakshin Dinajpur, Darjeeling, Jalpaiguri, Coochbehar) (Fig. 4.1). The spatial extent of the study area ranges between 87.79°–91.74 °E and 24.69°–28.09 °N and encapsulates a geographic area of 44,617.6 km^2. The varied topography and climatic conditions account for highly diverse flora (Champion and Seth 1968). The vegetation changes from tropical to subtropical upwards through middle hills with much coniferous and Oak forests of temperate character to the higher slopes with subalpine scrub and alpine “meadows” generally related to higher alpine flora of the north temperate zone (Singh and Sanjappa 2011).

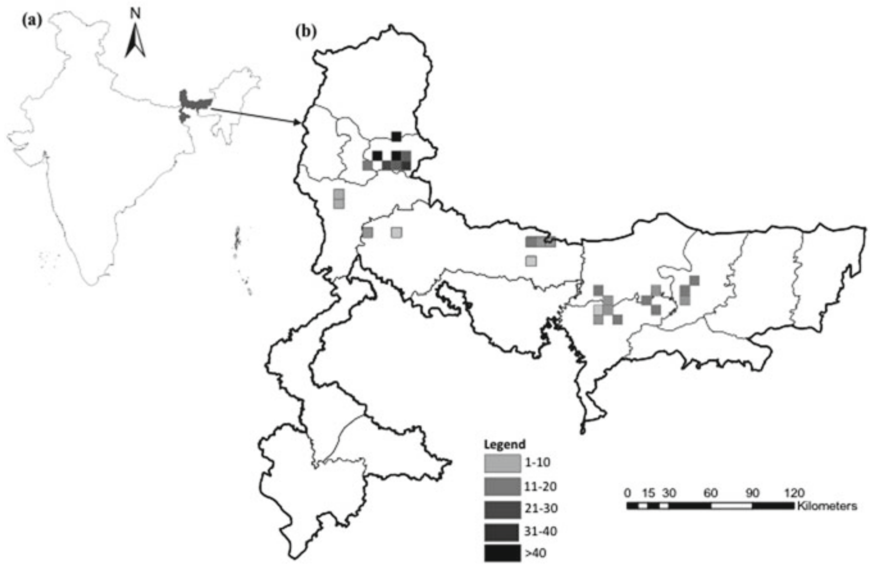

Fig. 4.1 **a** Map showing the study area along the foothills of Indian Himalaya, **b** the spatial distribution of sampled grids and the woody plant species richness ranging from 1 to 54

4.2.2 Biotic Determinants

The primary geo-tagged plants used for this study were collected under the project ‘Bioresources and Sustainable Livelihoods in Northeast India’ funded by the Department of Biotechnology, New Delhi, India. The entire study site was divided into 6.3 × 6.3 km^2 grid. The field inventory was carried out in the foothills of Himalaya that holds the diverse floristic composition and forest types. Moreover, the grid sampled for this study falls within the elevational range of 500–2200 m. The sampling of flowering plants were performed in each of the 6.3 × 6.3 km^2 grid using two belt transects of 10 m × 500 m. Tree species were enumerated in the entire belt transect and the shrub and herb layers were enumerated at the beginning and end of the transects by laying sub plots of 5 × 5 m^2 for shrubs and 1 × 1 m^2 for herbs. Girth at breast height (GBH) and height of the trees were measured and voucher specimens were collected for identification purposes. Further geographic coordinates (latitude and longitude), suite of environmental variables (elevation, temperature, rainfall, moisture, slope, and aspect) and habitat information (canopy cover, canopy height, litter cover, litter depth, invasive species, soil temperature, moisture, disturbance, human use, etc.) were also recorded from each transect as part of metadata collection.

4.2.3 Abiotic Determinants

The available global data on the four essential climatic variables and one topographic variable were used as representative of abiotic determinants, i.e., mean annual surface air temperature (°C), mean annual precipitation (mm), mean annual volumetric soil moisture (m^3/m^3), mean annual surface air relative humidity (%), and elevation (m). Precipitation is the accumulated liquid and frozen water, including rain and snow, that falls to the earth's surface. The determinants do not include fog, dew or the precipitation that evaporates in the atmosphere before it lands at the surface of the earth. Surface air temperature is the temperature of the air at 2 m above the surface of land. The temperature at 2 m level from the ground is calculated by interpolating between the lowest model level and the earth's surface, taking account of the atmospheric conditions. Volumetric soil moisture is the volume of water in soil layer 1 (0–7 cm, the surface is at 0 cm). The volumetric soil water is associated with the soil texture (or classification), soil depth, and the underlying groundwater level. Surface air relative humidity is the ratio of the partial pressure of water vapour to the equilibrium vapour pressure of water at the same temperature near the surface. The four essential climatic variables were downloaded ERA5 climate reanalysis from the Copernicus data portal (ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5). The downloaded climatic data were the monthly mean of each variable at the spatial resolution of $0.25° \times 0.25°$ for the year 2019. The elevation data was downloaded from Shuttle Radar Topography Mission (SRTM) digital elevation model at a spatial resolution of 90 m. The abiotic determinants mentioned henceforth include temperature, precipitation, soil moisture, relative humidity and elevation.

4.2.4 Data Preparation

A total of 27 transects were laid in the study site as one transect per 6.3×6.3 km^2 grid. For each transect, the g.b.h. was converted to d.b.h. by dividing the g.b.h. value with pi or 3.14. The woody species counts were made and tabulated for the d.b.h. $\geq$ 2.5 cm and d.b.h. $\geq$ 10 cm in each transect. Similarly, the tree heights were averaged for the total woody species in the transects for d.b.h. $\geq$ 2.5 cm. For this study, three biotic variables d.b.h. $\geq$ 2.5 cm, d.b.h. $\geq$ 10 cm and tree height were selected. Also, a record was created for the woody plants genera and family. On the other hand, the downloaded global ERA5 data of the four essential climatic variables were masked using the shapefile of the study sites in QGIS software. The data were normalized, averaged and calculated for each essential climatic variable. Zonal statistics analysis was performed using the essential climatic variables and integrated to each sampled grid of 6.3×6.3 km^2 grid.

4.2.5 *Statistical Analysis*

Spearman rank correlation (Rho) is a non-parametric correlation test that evaluates the multicollinearity of ecological determinants through the correlation matrix. We utilised both the ecological determinants (abiotic and biotic) against woody plant species richness using CRAN package "GGally" in R software. Two ecological determinants having Rho $\geq$ 0.7 are considered as co-linear. The subsequent analysis considered one out of those collinear determinants in the model, to avoid biases and overestimation. Thereafter, the linear regression model (LM) was performed between the ecological determinants and woody plant species richness.

The structural equation model (SEM) was used to evaluate the relationship between ecological determinants and woody plant species richness. SEM is a complex and robust regression model widely used in ecological analysis (Panda et al. 2017; Rana et al. 2019). The general methodology of SEM involves the specification of a multivariate dependence model that can be statistically tested against field data. In essence, the specification of a hypothesized model yields an expected covariance matrix that can be tested against the actual covariance matrix. Also, SEM allows the estimation of latent variables using multiple observed indicators and reports the measurement errors. This multivariate technique not only assists in selecting models among alternatives but also provides an efficient and simultaneous solution to a series of overlapping regression relationships (Daou and Shipley 2019).

The analysis was performed in R software using the packages namely "lavaan", "haven", and "semPlot" from CRAN repository.We compared each ecological determinant against woody plant species richness. Thereafter, we tested the combination of two, three, and four ecological determinants with the woody plant species richness. We restricted the SEM evaluation with four variables as thereafter the degree of freedom was found to be zero. The model performance was evaluated using the beta coefficient, R^2 value, root mean square error. Also, the covariance among the variables were evaluated.

4.3 Results

The primary woody plant data was collected from 27 transects sampled in 27 respective grids of size 6.3 $\times$ 6.3 km^2 in the Himalayan forests which are contiguous in Sikkim, West Bengal and Assam states, India. The Indian Himalayan forest has high spatial heterogeneity and hence from the foothills to an elevation of 2200 m harbors varied forest types and transition zones. The forest types encountered during this study are tropical, subtropical, temperate, along with the elevation ranges in ascending manner. These could also be classified as deciduous, mixed-deciduous, warm broadleaf, semi-evergreen and evergreen forest based on the vegetation types. The transect level woody plant species richness was found to range from 1 to 54/ha among the sampled transects from the study site (Fig. 4.1b). A total of 302 unique woody plants belonging to 233 genera were identified and recorded from the 27 sampled transects in the study site. The most abundant family to which the woody plants belonged are *Fagaceae*, *Theaceae*, *Dipterocarpaceae*, *Symplocaceae*, *Cupressaceae*.

The five most abundant woody plants such as *Shorea robusta* (561), *Terminalia bellirica* (167), *Tectona grandis* (140), *Mallotus philippensis* (128), *Melia azadirachta* (112) were recorded in the sampled transects from Assam. A total of 107 unique woody plants were recorded from the study sites of Assam. Similarly, the five most abundant woody plants *Castanopsis sp.* (310), *Viburnum erubescens* (231), *Symplocos sp.* (158), *Eurya cavinervis* (141), *Cryptomeria japonica* (116) were recorded in the sampled transects from Sikkim. A total of 151 unique woody plants were recorded from the study sites of Sikkim. The five most abundant woody plants *Shorea robusta* (99), *Machilus edulis* (79), *Magnolia champaca* (77), *Aglaia spectabilis* (67), *Tectona grandis* (41) were recorded in the sampled transects from West Bengal. A total of 82 unique woody plants were recorded from the study sites of West Bengal.

Among the abiotic determinants, mean annual temperature ranged from −5.5 to 25.5 °C in the study site for the year 2019 (Fig. 4.2a). The low to medium range of temperature pattern was observed in Sikkim, whereas higher range of temperature was recorded for forests in the Assam and West Bengal states (Fig. 4.2a). The annual mean precipitation was found to range from 584 to 7650 mm. The range of medium

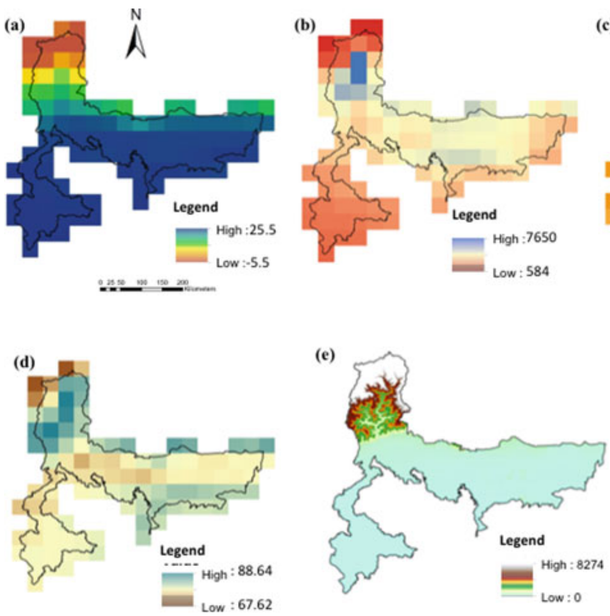

Fig. 4.2 Representing the abiotic determinants selected for this study, i.e., **a** temperature (°C), **b** precipitation (mm), **c** soil moisture in m^3/m^3, **d** relative humidity (%), and **e** elevation (m)

to high precipitation was recorded for forests in Sikkim and Assam states, except the snow covered area of Sikkim. The low to medium level precipitation was recorded in the forests of West Bengal state (Fig. 4.2b). The volumetric soil moisture was found to range from 0.21 to 0.42 m^3/m^3. The soil in the forests of Sikkim and Assam states had high soil moisture holding capacity compared to the forests of West Bengal (Fig. 4.2c). The relative air humidity recorded for the study site was found to be ranging from 67.62 to 88.64%. Similar to the pattern of soil moisture, the relative air humidity was higher for Sikkim and Assam, while it was low to medium in the forests of West Bengal state (Fig. 4.2d). The mean elevation of the grids for the study site was found to be ranging from 0 to 8274 m. The majority of higher elevational variation was recorded in the Sikkim region, whereas the Assam and West Bengal regions varied from moderate elevation to plain (Fig. 4.2e).

The Spearman rank correlation test was performed among and within the ecological determinants and woody plant richness. The resulting correlation matrix was found to be ranging from −1 to + 1 (Fig. 4.3). The woody plant species richness was

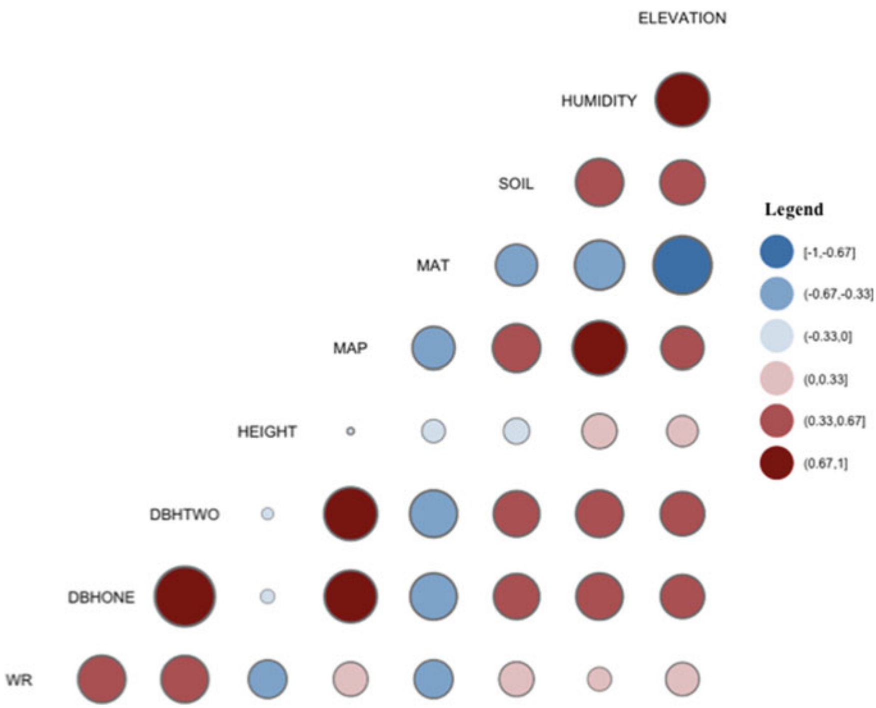

Fig. 4.3 The result from Spearman rank correlation performed between and among woody plant species richness and ecological determinants are represented as a correlation matrix and the range varies from −1 to +1. (WR—woody plant species richness, DBHONE—density d.b.h. ≥ 2.5 cm, DBHTWO—density d.b.h. ≥ 10 cm, HEIGHT—Tree height, MAP—Mean annual precipitation, MAT—mean annual temperature, SOIL—soil moisture, HUMIDITY—relative humidity, ELEVATION—elevation)

found to be moderately correlated with the two biotic determinants namely density d.b.h. ≥ 2.5 cm and density d.b.h. ≥ 10 cm (Fig. 4.3). However, the correlation between woody plant species richness and tree height was observed to be moderately negative. Among the abiotic determinants precipitation, soil moisture, relative humidity and elevation have resulted in low positive correlation with woody plant species richness. However, the woody plant species richness was negatively correlated with temperature (Fig. 4.3). The ecological determinants were found to be positively correlated among each other, except tree height and temperature. Due to high collinearity (Rho ≥ 0. 7) between density d.b.h. ≥ 2.5 cm and density d.b.h. ≥ 10 cm, one out of these determinants may be considered for better model representation (Fig. 4.3).

A comparison was made between LM and SEM to evaluate the relationship between woody plant species richness and individual ecological determinants. It was observed that the SEM outputs were statistically significant and the obtained root mean square error (RMSE) was <0.08 for each tested model using SEM (Table 4.1). Among the biotic determinants, the density d.b.h. ≥ 2.5 cm and density d.b.h. ≥ 10 cm individually resulted in highest significance ($R^2 = 0.4$) and slope (0.6) with woody plant species richness (Fig. 4.4b, d). However, the tree height showed the significance of ($R^2 = 0.15$) and negative slope (−0.34) with the woody plant species richness (Fig. 4.4f). Among the abiotic determinants, temperature resulted in highest significance ($R^2 = 0.15$) and a negative slope (−0.39) with woody plant species richness (Fig. 4.4h). However, the remaining abiotic determinants exhibited a significance of $R^2 \leq 0.1$ and positive slope ≤0.31 with woody plant species richness in the Indian Himalayan forest (Table 4.1; Fig. 4.4j–p).

SEM was performed using two ecological determinants (density d.b.h. ≥ 2.5 cm and tree height) against woody plant species richness exhibited highest significance of $R^2 = 0.49$ (Table 4.1; Fig. 4.5a). The model-I showed positive slope of 0.59 with density d.b.h. ≥ 2.5 cm and negative slope of −0.39 with tree height. Also, the model-J showed significance of $R^2 = 0.49$ considering density d.b.h. ≥ 10 cm and tree height against woody plant species richness. However, the observed slopes were 0.58 for density d.b.h. ≥ 10 cm and −0.36 for tree height with woody plant species richness (Table 4.1; Fig. 4.5b). The model-K considered the density d.b.h. ≥ 2.5 cm and precipitation against woody plant species richness and resulted in a significance of $R^2 = 0.37$. However, the positive slope of 0.63 was observed by density d.b.h. ≥ 2.5 cm and negative slope of −0.04 was observed for precipitation with the woody plant species richness (Table 4.1; Fig. 4.5c).

In model-O, SEM performed using three ecological determinants (density d.b.h. ≥ 2.5 cm, tree height, and precipitation) exhibited highest significance ($R^2 = 0.53$) in explaining woody plant species richness (Table 4.1; Fig. 4.6a). Moreover, a positive slope of 0.72 was observed for density d.b.h. ≥ 2.5 cm, while tree height (−0.44), and precipitation (−0.25) exhibited negative slope (Fig. 4.6a). Similarly, the model-P (density d.b.h. ≥ 2.5 cm, tree height, relative humidity) and model-Q (density d.b.h. ≥ 2.5 cm, tree height, elevation) resulted in significance of $R^2 = 0.51$ and $R^2 = 0.50$, respectively (Table 4.1; Fig. 4.6b, c). The model-T, analysed a combination of four ecological determinants (density d.b.h. ≥ 2.5 cm, tree height, elevation, relative

Table 4.1 Representing the significant outputs (root mean square error <0.08) from the structural equation model (SEM), where different combinations of ecological determinants were tested against woody plant species richness (WR)

Model	Combinations of ecological determinants	R^2
WR versus one ecological determinant		
A	WR ~ density d.b.h. ≥ 2.5 cm	0.4
B	WR ~ density d.b.h. ≥ 10 cm	0.4
C	WR ~ tree height	0.15
D	WR ~ temperature	0.15
E	WR ~ precipitation	0.10
F	WR ~ soil moisture	0.10
G	WR ~ relative humidity	0.10
H	WR ~ elevation	0.02
WR versus two ecological determinants		
I	WR ~ density d.b.h. ≥ 2.5 cm + tree height	0.49
J	WR ~ density d.b.h. ≥ 10 cm + tree height	0.49
K	WR ~ density d.b.h. ≥ 10 cm + precipitation	0.37
L	WR ~ density d.b.h. ≥ 2.5 cm + density d.b.h. ≥ 10 cm	0.36
M	WR ~ tree height + temperature	0.34
WR versus three ecological determinants		
N	WR ~ density d.b.h. ≥ 2.5 cm + tree height + precipitation	0.53
O	WR ~ density d.b.h. ≥ 2.5 cm + tree height + relative humidity	0.51
P	WR ~ density d.b.h. ≥ 2.5 cm + tree height + elevation	0.50
Q	WR ~ density d.b.h. ≥ 2.5 cm + tree height + soil moisture	0.50
R	WR ~ density d.b.h. ≥ 2.5 cm + tree height + temperature	0.50
S	WR ~ density d.b.h. ≥ 2.5 cm + density d.b.h. ≥ 10 cm + tree height	0.49
WR versus four ecological determinants		
T	WR ~ density d.b.h. ≥ 2.5 cm + tree height + relative humidity + elevation	0.56
U	WR ~ density d.b.h. ≥ 2.5 cm + tree height + relative humidity + temperature	0.55
V	WR ~ density d.b.h. ≥ 2.5 cm + tree height + precipitation + Elevation	0.54

(continued)

Table 4.1 (continued)

Model	Combinations of ecological determinants	R^2
W	WR ~ density d.b.h. ≥ 2.5 cm + tree height + precipitation + temperature	0.54
X	WR ~ density d.b.h. ≥ 2.5 cm + tree height + precipitation + relative humidity	0.53
Y	WR ~ density d.b.h. ≥ 2.5 cm + tree height + precipitation + soil moisture	0.53

humidity) using SEM can be considered as the best model ($R^2 = 0.55$) to explain woody plant species richness of the Indian Himalayan forest (Table 4.1; Fig. 4.7a). The positive slope was observed for density d.b.h. ≥ 2.5 cm (0.67) and elevation (0.36), whereas negative slope was observed for tree height (−0.30) and relative humidity (−0.45; Fig. 4.7a). The model-U resulted in the significance of $R^2 = 0.54$ in explaining woody plant species richness of the Indian Himalayan forest (Table 4.1; Fig. 4.7b).

4.4 Discussion

The ecological determinants tested individually against woody plant species richness observed that biotic determinants ($R^2 \leq 0.4$) are more significant than abiotic determinants in explaining the patterns ($R^2 \leq 0.15$; Fig. 4.4). Among all the abiotic determinants, temperature significantly explained the woody plant species richness; that corroborates with the study performed by Basnett et al. (2019) to evaluate phenological traits of woody plant species. Moreover, they defined no significant role of elevation. Similarly, our study also observed a poor fit ($R^2 \leq 0.1$) between woody plant species richness and elevation (Fig. 4.4n). In contrast, Pandey et al. (2018) found the highest woody plant species richness at an elevation of 1000 m and summarized elevation as a significant abiotic determinant. Probably, scale dependent characteristics of ecological determinant must be considered to compare the observation made for woody plant species richness (Asner et al. 2017; Li et al. 2019). Moreover, our field inventory made up to the mean elevation of 2200 m out of 8274 m. Therefore, considering the woody species occurrence from the whole elevation range can better explain the variation along elevation. The remaining abiotic determinants such as precipitation, relative humidity and soil moisture tested individually against woody plant species richness exhibited a poor fit ($R^2 \leq 0.1$) with a positive slope.

The best combination of two ecological determinants were density d.b.h. ≥ 2.5 cm and tree height, although these two are biotic determinants. This summarised that the significance of two biotic determinants is higher than any other combinations (Table 4.1). On the other hand, the combinations of three ecological determinants such as density d.b.h. ≥ 2.5 cm, tree height and precipitation is observed to be the best model compared to other combinations. It can be summarised that the combined effect of

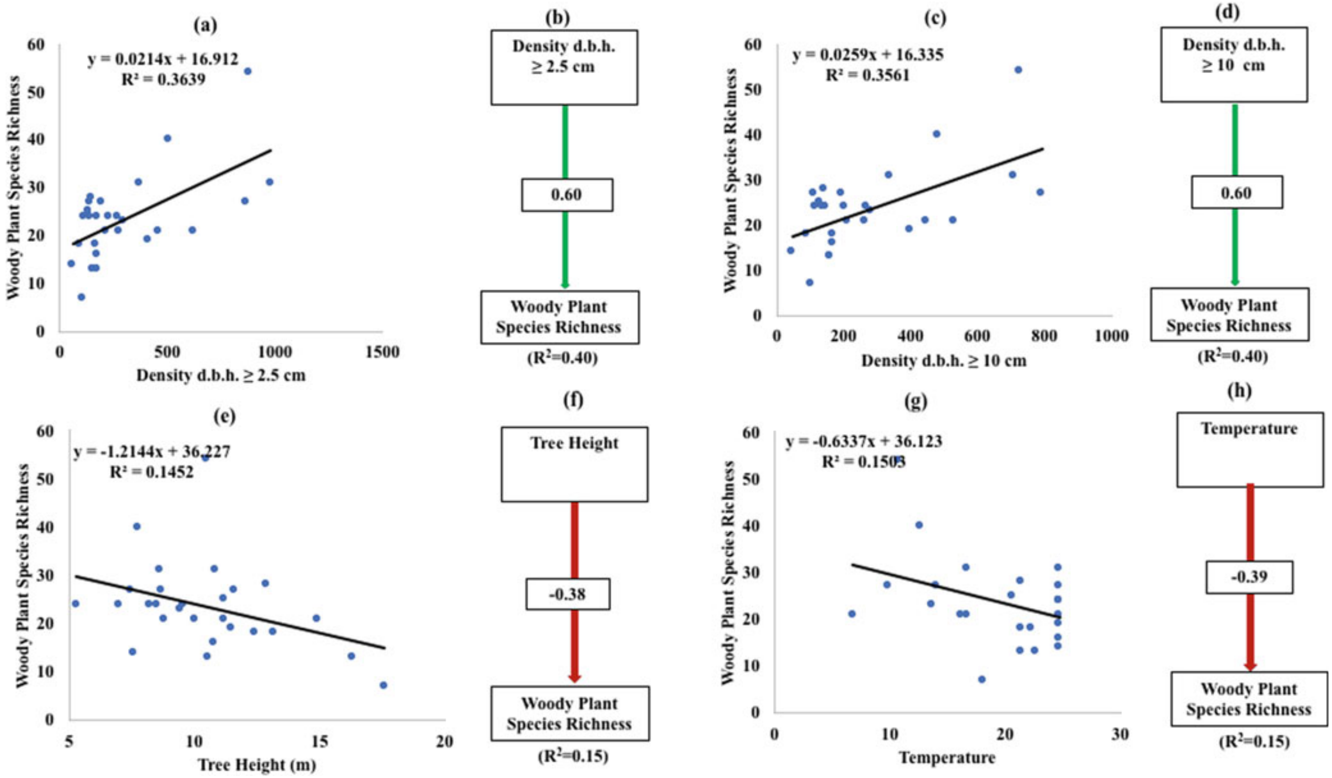

Fig. 4.4 Comparison of linear regression model (**a**, **c**, **e**, **g**, **i**, **k**, **m**, **o**) and structural equation model-SEM (**b**, **d**, **f**, **h**, **j**, **l**, **n**, **p**) by evaluating the significance (slope, R^2) of woody plant species richness against individual ecological determinants

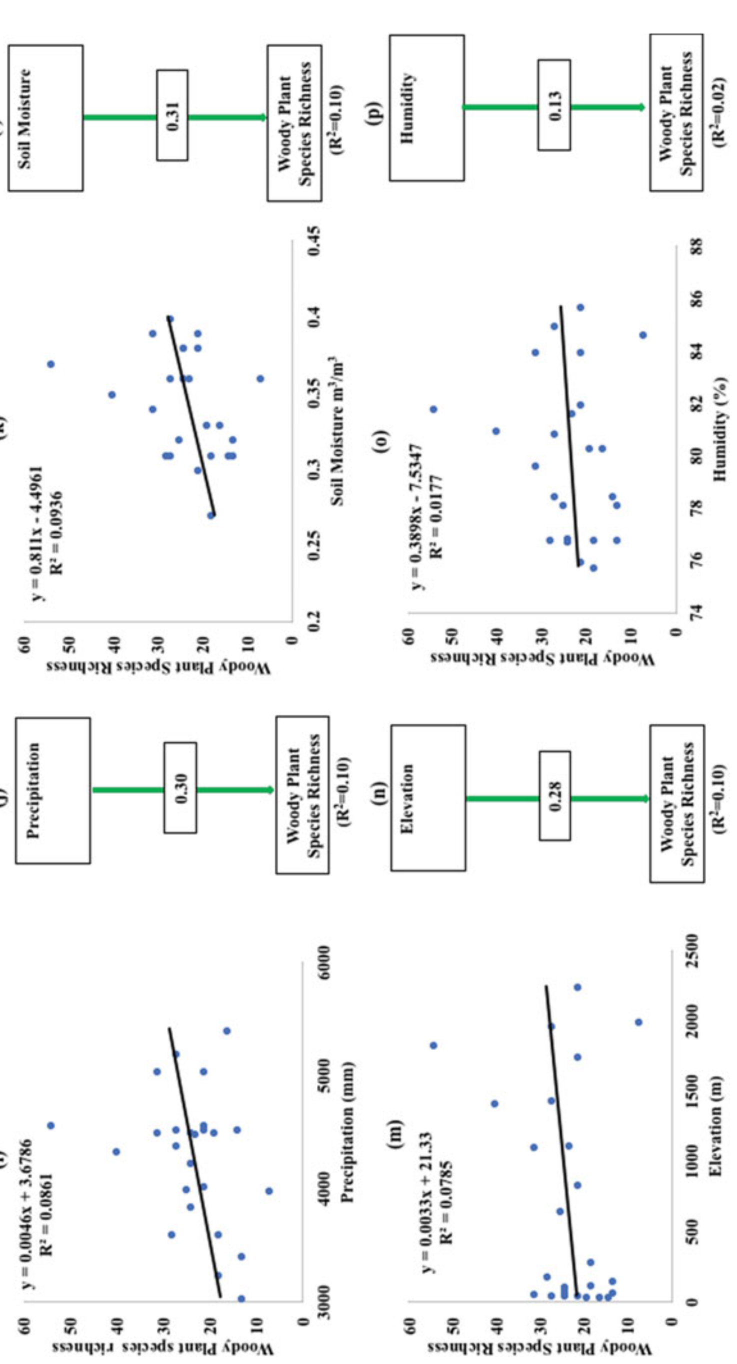

Fig. 4.4 (continued)

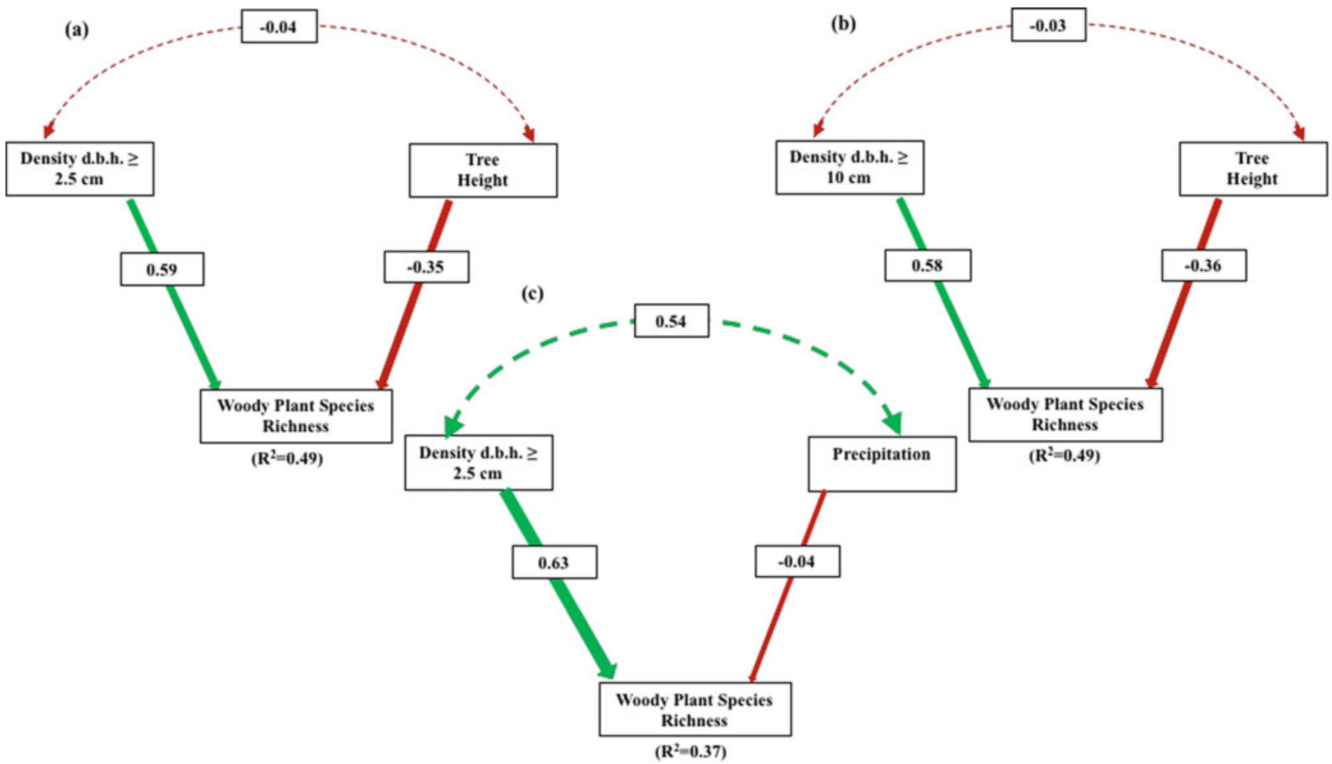

Fig. 4.5 SEM output to evaluate the significance of two ecological determinants, **a** density d.b.h. ≥ 2.5 cm and tree height (two biotic determinants), **b** density d.b.h. ≥ 10 cm and tree height (two biotic determinants), **c** density d.b.h. ≥ 2.5 cm and precipitation (one biotic and one abiotic determinants) in explaining woody plant species richness of the Indian Himalayan forest (where, solid line-slope dotted line-covariance, red colour-negative slope/covariance, green colour-positive slope or covariance)

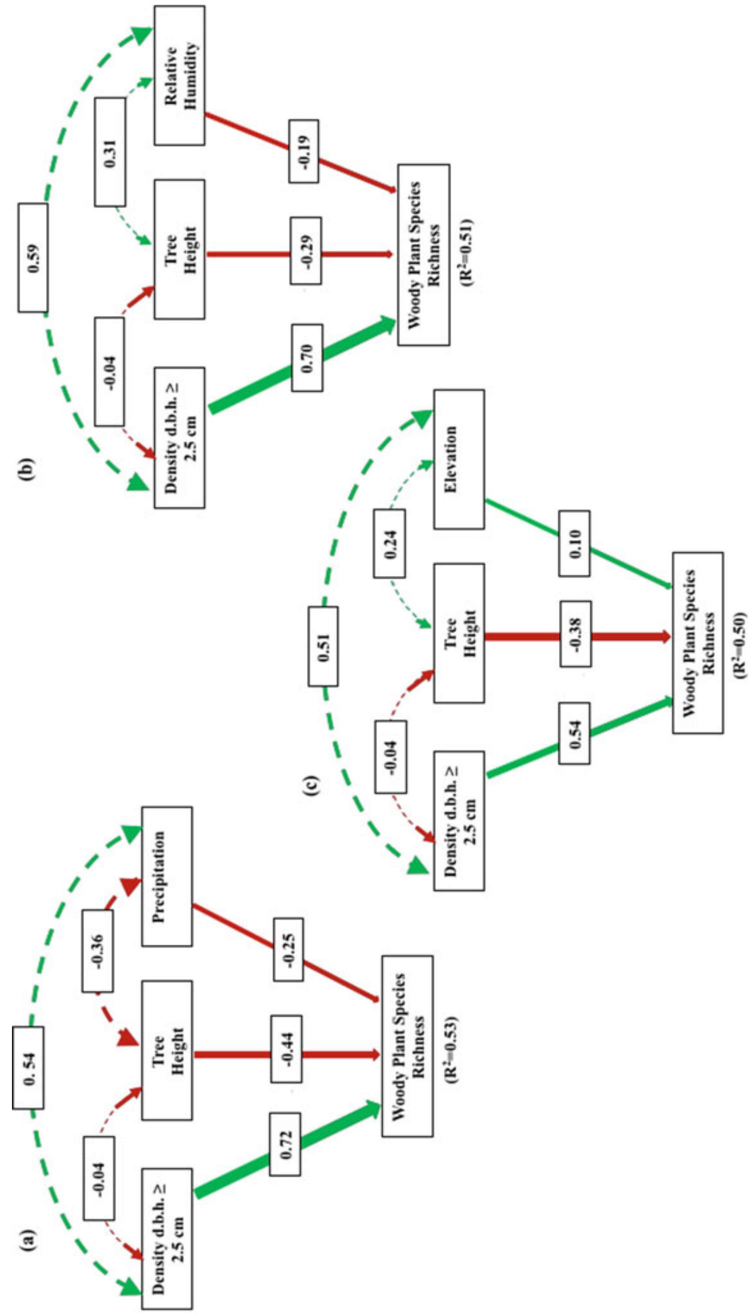

Fig. 4.6 SEM output to evaluate the significance of three ecological determinants, i.e., **a–c** utilized two biotic and one abiotic determinants against the woody plant species richness of the Indian Himalayan forest

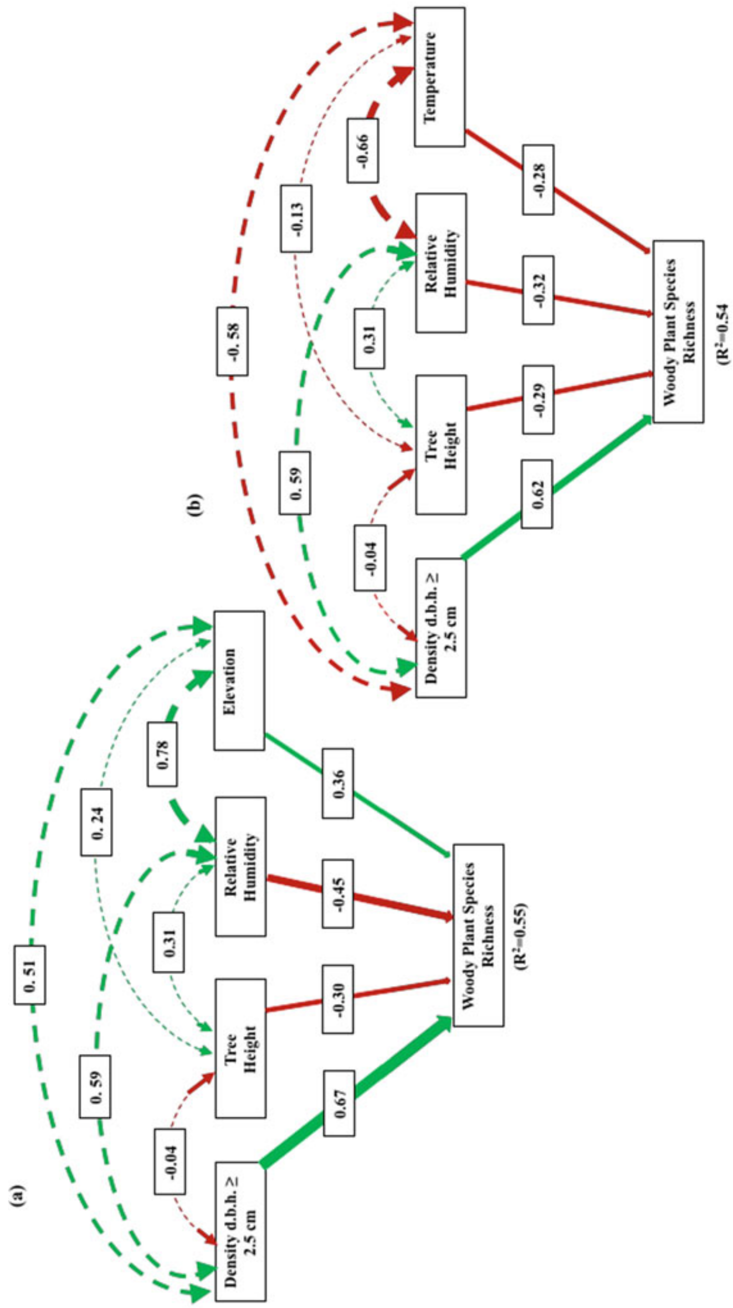

Fig. 4.7 SEM output to evaluate the significance of four ecological determinants (two biotic and two abiotic) as showin in **a** and **b** to explain woody plant species richness of the Indian Himalayan forest

both biotic and abiotic determinants is a good explanation. However, the combination of four ecological determinants d.b.h. $\geq$ 2.5 cm, tree height, relative humidity and elevation emerged as the best combination to explain woody plant species richness in the Indian Himalayan forest. These observations can be validated with inferences made by Austin and Smith (1990) and Pau et al. (2012) that distribution of woody plant species richness can be determined partly by abiotic and partly by biotic determinants. Also, the similar observations were made by Saikia et al. (2017) that the high species richness can be explained by elevation and other ecological determinants and not by any sole factor. The study summarised that the combination of three ecological determinants can be the second best approach to understand the woody plant species richness. However, the best combination includes four ecological determinants (both biotic and abiotic) to explain woody plant species richness for the study site in the Indian Himalaya forest. Overall, the study infers that both biotic and abiotic determinants combined together better explain the woody plant species richness of Indian Himalayan forest, than individual abiotic and biotic determinants independently.

4.5 Conclusions

The main objective of the study was to evaluate the ecological determinants (abiotic, biotic) for woody plant species richness in the Indian Himalayan forest. Using SEM, the tested ecological determinants showed that, integration of biotic and abiotic determinants could outperform in explaining woody plant species richness. Probably, more field inventories for biotic determinants and higher resolution of abiotic determinants could enhance their significance to explain the woody plant species richness. However, field inventory in Indian Himalayan forest is subjected to various challenges (economic, time, labour), whereas high resolution abiotic determinants are not accessible publicly. The present study utilized the best available resources and summarizes the suitable combinations of ecological determinants, i.e., d.b.h. $\geq$ 2.5 cm, tree height, relative humidity, elevation for understanding woody plant species richness of the Indian Himalayan forest. Also, it emphasizes the strength of both biotic and abiotic determinants together, which can be considered to carry out similar studies in future.

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