

Plant species richness pattern across India's longest longitudinal extent

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Although the longitudinal pattern of biological diversity may not be as striking as the latitudinal pattern, there are climatic gradients associated with habitat, topography, and disturbance, which may generate variation in biological diversity along a longitudinal extent. We analysed the pattern of plant diversity using field data gathered from a national level 'biodiversity characterization at landscape level' project, along the longest longitudinal extent of India, varying from desert to wet tropics. Across a 3° latitudinal band (25–27°N lat.), the aridity decreased drastically from west to east, and the vegetation varied from tropical thorn, tropical deciduous, tropical semi-evergreen to tropical evergreen forests. In general, the species diversity is maximum in the east, minimum in the centre and intermediate in the west. The proportion (with respect to total number of species of each corresponding grid) of woody trees increased by half and shrubs increased by one-third, whereas herbal proportion decreased by half from western to eastern grid. The major predictor of species richness was the number of forest vegetation types, followed by topography (ruggedness index); together these explained 63% of the variance as revealed from generalized linear modelling analysis. The study concludes that, from west to east, (i) the vegetation type varies from tropical thorn to tropical moist/wet evergreen forest corresponding to aridity; (ii) there is monotonic drastic increase of woody tree, moderate increase of shrub, and drastic decrease of herb species, and (iii) plant diversity has a nonlinear distribution pattern attributed mainly to variation in the number of forest vegetation types followed by abiotic topography and climate. The study was possible due to the availability of national plant diversity database that followed a uniform field sampling design.

Keywords: Aridity index, climate, disturbance, plant life form, topography, vegetation type.

PATTERNS of species distribution are a product of many processes, including species history (speciation, migration and extinction), geographic location, and environmental variables (geology, topography, climate and soil).

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Earth–Sun relationships (axial tilt, orbital cycle, etc.) and abiotic planetary factors (surface physiography, atmospheric circulation, etc.) determine spatio-temporal variations in climate. The former always produce a latitudinal gradient in the duration and intensity of incoming solar energy, and thus the first-order pattern of variation in climate. The latter modify this pattern, more prominently over continental scales, where climate varies along an essentially longitudinal gradient¹. Although latitudinal patterns in species diversity are well known², relatively little is known about the diversity patterns along a longitudinal gradient. While longitudinal patterns of biological diversity may not be as striking as the latitudinal pattern (since the latter is associated with large climatic differences from the poles to the equator), there are climatic gradients associated with coastal to interior areas, such as precipitation and temperature, which are expected to give rise to variation in biological diversity along a longitudinal gradient³.

The few studies of longitudinal patterns in diversity can be summarized briefly. In North America Qian⁴ found that the alpha diversity of boreal forest changes from west to the east in an asymmetric modal trend. O'Brien⁵ argued that the woody plant species richness tends to increase from west to east across southern Africa in a non-latitudinal, essentially longitudinal fashion; consistent with the increasing dominance of woody plants as vegetation shifts from desert to evergreen forest. Karrenberg *et al.*⁶, working within the active zone of the near-natural Tagliamento, NE Italy, found that diversity of woody vegetation was mainly structured by the longitudinal gradient, which corresponded to gradients in air temperature and altitude. Spatial patterns in riparian vegetation composition and structure also occur along longitudinal gradients within river catchments⁷. For the semi-arid San Pedro river flood plain, Lite *et al.*⁸ suggested that species richness varies along longitudinal gradients with changes in surface and groundwater availability, canopy cover and topographic diversity.

India is a vast and topographically varied subcontinent that extends from the tropics to the sub-tropics. Along its northern span, the Thar desert bounds India on the west, the Gangetic plains compose the middle, and the eastern Himalaya and the Brahmaputra valley form the easternmost boundary (Figure 1). This provides a gradient of arid, semi-arid, tropical dry, tropical moist, subtropical humid and montane climate from west to east. The arid climate of the Thar desert in the west allows the growth of xerophytes and dry succulents. The central Gangetic plains are characterized by semi-arid vegetation in the west, moist deciduous and evergreen species in the north and dry deciduous species in the south. The eastern Himalaya and the Brahmaputra valley support tropical semi-evergreen and evergreen species in the lower elevations, and moist or wet evergreen species of temperate and alpine zones in the elevated highlands⁹. The altitudinal

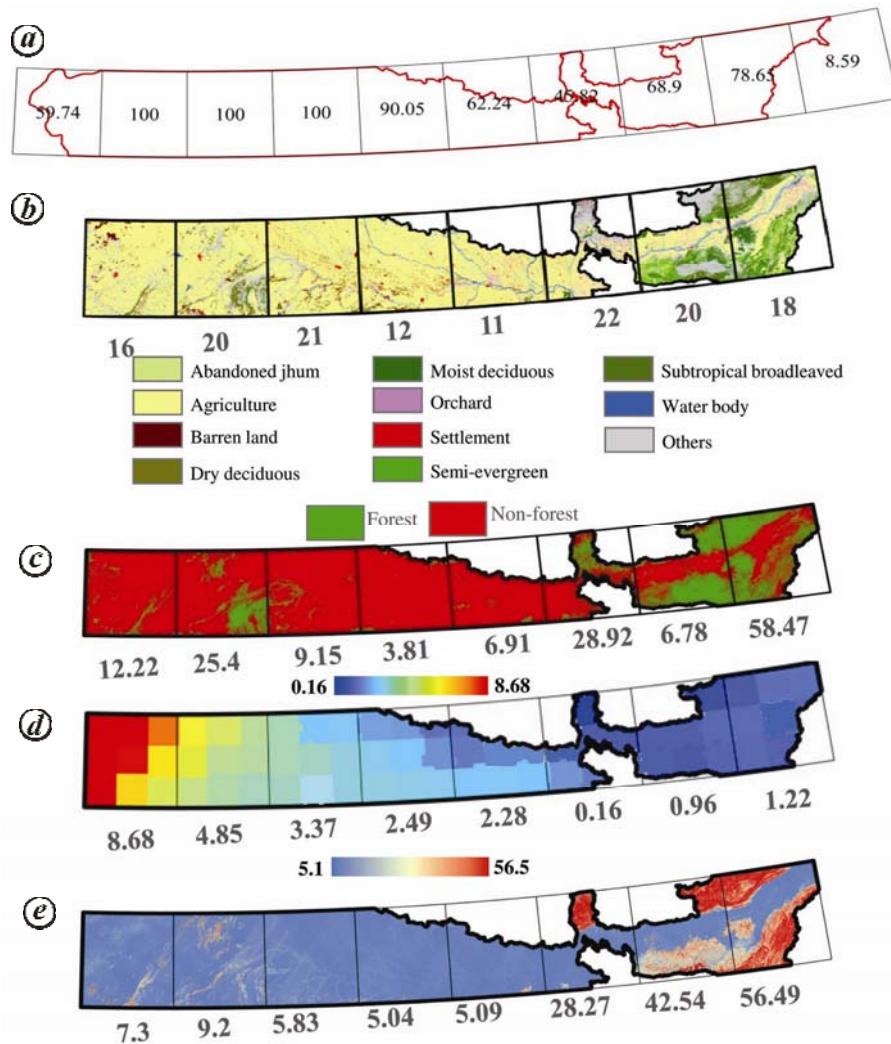


Figure 1. *a*, Grid-wise geographic area; *b*, Number of forest vegetation cover types (serial numbers of the legends in the vegetation type map corresponds to those mentioned in Table 1); *c*, % Forest cover; *d*, Aridity index; *e*, Terrain ruggedness index.

gradient in the eastern Himalaya gives rise to a varied moisture regime that supports a diversity of trees, shrubs, herbs and lianas¹⁰.

In this study, we describe the pattern of plant diversity along India's longest longitudinal extent, and also investigate how climate, topography, habitat heterogeneity and disturbance factors may explain the variation in diversity.

For this study, we chose a 3° (25–27°N) lat. band between 70° and 96°E long. in order to pick the longest possible continuous longitudinal extent across the country (Figure 1). Within this band, we used a fixed 3° × 3° grid size, starting at India's easternmost boundary of 68°E long. (Figure 1*a*). However, the easternmost and westernmost grids were excluded from our analysis because of incompleteness (Figure 1*b–e*). To analyse the distribution of species diversity, we used the plant diversity database generated in an 'Indian national project entitled Biodiversity characterization at landscape level'; in con-

sideration with the forest vegetation type distribution⁹ (Table 1; Figure 1*b*). We recoded the forest vegetation types to derive forest and non-forest map (Figure 1*c*). Images from Indian remote sensing satellites were utilized for vegetation-type delineation and mapping¹¹. On-screen visual interpretation technique was adopted for vegetation and land-cover mapping, as it provided optimum accuracy (>90%) due to control over individual polygon delineations¹¹. The field sampling intensity (i.e. proportion of area under each vegetation type that was sampled) was maintained between 0.002% and 0.005% for vegetation types¹². Global positioning system receivers were utilized for locating field sample plots, gathering location attributes of plant species and providing field-points for assessing the classification accuracy of the vegetation-type map. A geographic information system (GIS) was used to link the phyto-database based on field sampling records with vegetation and land-cover types¹².

RESEARCH COMMUNICATIONS

Table 1. Vegetation type distribution pattern along 3° × 3° grids (adapted from Roy *et al.*¹¹)

Forest vegetation type	Mid-value of 3° longitudinal grid							
	72	75	78	81	84	87	90	93
Mixed forest formations	1. Tropical evergreen							x
	2. Subtropical broadleaved evergreen						x	x x
	3. Montane wet temperate						x	
	4. Himalayan moist temperate						x	x x
	5. Sub-alpine						x	x x
	6. Tropical semi-evergreen							x x
	7. Tropical moist deciduous				x	x x	x	x x
	8. Tropical sal mixed moist deciduous				x	x x	x	
	9. Tropical teak mixed moist deciduous				x	x	x	x
	10. Tropical dry deciduous	x	x	x	x	x x	x	
	11. Tropical sal mixed dry deciduous					x	x	
	12. Tropical thorn	x	x	x				
	13. Temperate coniferous						x	x x
Gregarious forest formations	14. <i>Shorea</i> spp.					x	x	
	15. <i>Tectona grandis</i>							x
	16. <i>Dipterocarpus</i> sp.							
	17. <i>Bamboo</i> spp.						x	x
	18. <i>Pinus</i> spp.							x x
	19. <i>Abies</i> spp.							x x
	20. <i>Pterocarpus santalinus</i>	x	x					
	21. <i>Boswellia</i> spp.		x	x				
	22. <i>Anogeissus pendula</i>		x	x				
	23. <i>Rhododendron</i> spp.						x	
Locale-specific formations	24. <i>Xylocarpus</i> spp.		x					
	25. Lowland swamp forest					x		
	26. Riverine		x				x	x
	27. Tropical seasonal swamp forest					x		
Forest plantations	28. Forest plantation	x						x
	29. <i>Eucalyptus</i> spp.	x	x	x				
	30. <i>Alnus</i> spp.		x				x	
	31. Mixed plantation				x	x		
Degraded forest	32. Degraded forest		x	x	x	x	x	x x
	33. Abandoned jhum	x	x	x				x x
	34. Current jhum							x
Woodland	35. Tree savannah			x	x			
	36. Shrub savannah		x					
Shrub/scrubland	37. Dense scrub		x	x	x		x	x x
	38. Open scrub			x	x		x	
	39. Dry deciduous scrub		x	x	x	x	x	
	40. <i>Ziziphus</i> spp. dominant				x			
	41. Moist alpine scrub							x x
	42. <i>Prosopis juliflora</i>	x		x	x			
	43. <i>Lantana</i> sp. dominant	x	x	x				
	44. Desert dune scrub	x	x					
Grassland	45. Thorn scrub			x				
	46. <i>Prosopis cineraria</i>	x	x					
	47. Grassland							x x
	48. Riverine				x	x		
	49. Swampy land			x				x
	50. <i>Lasiurus-Panicum</i> spp.	x				x		
	51. <i>Cenchrus-Dactyloctenium</i> sp52p.	x	x					
	52. Coastal swampy		x					
Managed ecosystems	53. Orchard			x	x		x	x x
	54. <i>Camelina</i> spp.						x	x
	55. <i>Mangifera</i> spp.				x			
	56. <i>Crocus sativus</i>			x				
	57. <i>Cryptomeria</i> spp.	x					x	
	58. <i>Padauk</i> spp.	x	x					

Table 2. Number of species with their life-form break-up shown for every 3° × 3° grid (mid-longitude values are shown in bold)

	Life form Mid-value of 3° longitudinal grid							
	72	75	78	81	84	87	90	93
Lianas	29	33	24	13	8	54	42	61
Herb	238	316	250	65	90	372	204	262
Shrub	82	105	103	49	51	225	149	283
Tree	92	122	129	86	67	281	203	399
All species	441	576	506	213	216	932	598	1005

Details of the mapping methodology and description of vegetation types and field database enumeration are provided in Roy *et al.*⁹.

We calculated the percentage of occupied (=Indian) geographic area within the 3° grid for all the eight-grids, since they are expected to differ in each grid according to their area occupancy (Figure 1a). Further, for each 3° grid, we derived (a) percentage of forest area (FA) out of the occupied geographic area in that particular grid (which is same for three full LH grids and varies for rest of the grids) to estimate the habitat availability; (b) number of forest vegetation types (VT; Table 1), and (c) total number of species with their life form (Table 2).

We analysed the relationship between plant diversity and four predictor variables, i.e. forest area, number of forest vegetation types, climatic and topography for the grids. In terms of climate, we calculated an aridity index, $AI = 100T/P$, where T is the average annual temperature (°C); and P is the average annual rainfall (mm)¹³. Index values can be interpreted as follows (with reference to ref. 13, Spain): $AI < 2$, wet-humid, $AI 2-3$, semi-arid, $AI 3-6$ arid, and $AI > 6$, extremely arid or desert. Temperature and rainfall were calculated by simple averaging of the 0.5° × 0.5° gridded data from the climate research unit (CRU) dataset¹⁴ during 1950 to 2006 (Figure 1d). The open-source GIS software GRASS (geographic resources analytical support system) was used on Linux operating system to convert the CRU datasets into GRASS raster data layers. GRASS GIS modules along with Linux scripting were used to extract the annual average rainfall.

In addition to climate, we also calculated a terrain ruggedness index (RI)¹⁵ (Figure 1e) using SRTM (Shuttle Radar topographic Mission)-derived elevation information. RI expresses the amount of elevation difference between adjacent cells of a digital elevation grid. Since anthropogenic disturbance could also influence plant diversity, we accounted for forest cover percentage (in proportion to forest plus non-forest area within the Indian territory) through a forest map. This measures the proportion of natural versus human-modified habitats in each grid as an index of disturbance (Figure 1c).

We used scatter plots to examine the univariate relationships between species richness (number of species) on the one hand and four predictor variables: number of

forest vegetation types, forest area, ruggedness index, and aridity index on the other. This was followed by generalized linear modelling (GLM) with Poisson error distribution, in which all four predictors were examined simultaneously. This analysis was carried out using R (version 3.1.10). To assess the relative importance of the predictors, each predictor was excluded in turn, and subsequent model fit compared with the full model.

A total of 58 forest vegetation types consisting of natural, semi-natural and managed formations clubbed under nine broad categories were distributed along the longitudinal extent (Table 1). Degraded forests were distributed in all eight grids, whereas tropical moist deciduous and tropical dry deciduous forests were distributed in seven and six grids respectively (Table 1). In general, as we move from west to east, the dominant vegetation occurrences are tropical thorn, tropical deciduous, tropical semi-evergreen and tropical evergreen forests. However, subtropical, temperate and sub-alpine forests are seen in the three easternmost grids (Figure 1b). We observed desertic scrubland and grasslands in the two westernmost grids, whereas alpine scrub and grasslands were found in the two easternmost grids. Dry deciduous scrubland was found in the six western grids, while the central four grids accommodated swampy and riverine grasses (Table 1). Fourteen vegetation classes have very localized distribution, being found in only one grid. Vegetation types vary from non-woody dominants in the desert in the west, to evergreen forests with woody dominants in the eastern Himalaya (Table 2). Per cent forest area was the highest in the 92°–94°E long. grid (62.44), followed by the 89°–91°E long. grid (45.03); and reached a minimum at the 80°–82°E long. grid (3.88; Figure 1b). The number of different vegetation types in a grid varied from 11 to 22, with the 86°–88°E long. grid containing the highest number of vegetation types, even though the forest occupies only 19% of available area in that grid (Figure 1b). This large number is mostly contributed by a single sub-grid of Sikkim in the Himalayas (Figure 1b), and is due to the presence of tropical dry forests in the foothills, moist/wet tropical to temperate and sub-alpine forests, and alpine shrub/grassland in the highlands of the eastern Himalaya (Table 1). The easternmost grid had the maximum FA (58.47%), whereas the middle Gangetic grids had <10%

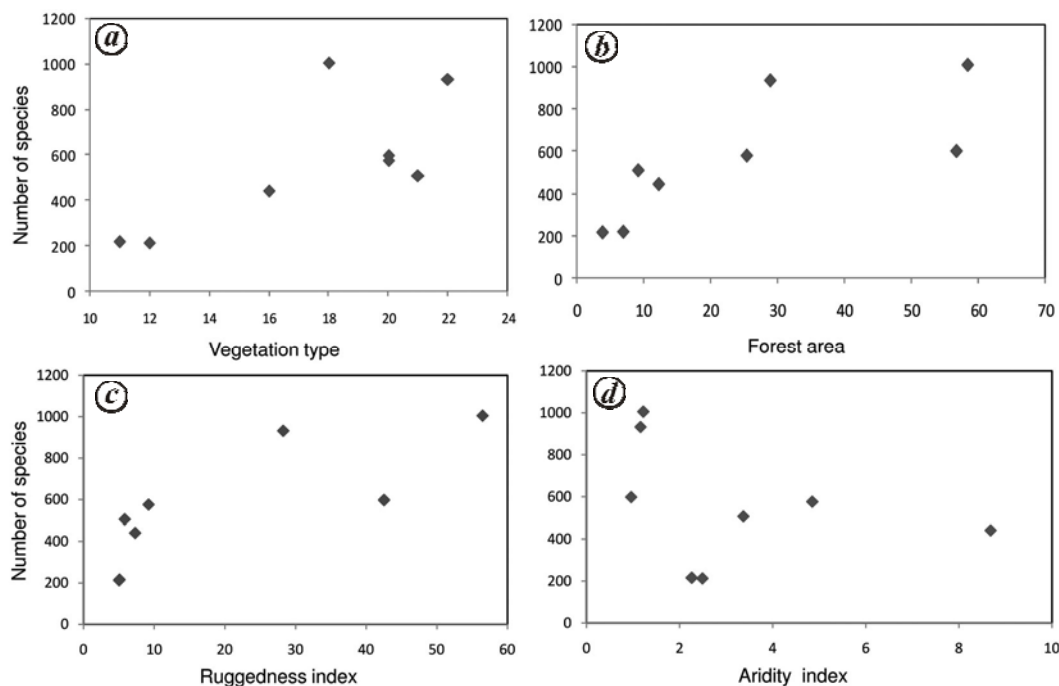


Figure 2. Scatter plots showing nonlinear relationship between species diversity (i.e. number of species) with (a) vegetation type, (b) forest area, (c) ruggedness index and (d) aridity index, using second-order polynomial curve fitting. Aridity index is negatively correlated with species diversity, indicating limiting role of climate on species distribution along India's longest longitudinal extent.

FA, indicating disturbance (Figure 1 c). AI decreased drastically from west to east, i.e. from 8.68 to 0.16 (Figure 1 d). RI varied from 5.1 to 56.5, with the three easternmost grids having the largest values due to the presence of Himalayan mountain (all above 28; Figure 1 e).

In general, the total number of species as well as woody species (trees, lianas) was the maximum in east (Table 2). The species diversity appears to fluctuate from west to east, increasing from the arid to the semi-arid region, then decreasing in the tropical dry region of the Gangetic plains, followed by a sudden increase in the tropical wet, subtropical humid and highland climate of the east. The proportion of herbs (with respect to the total number of species in that grid) decreases drastically from west to east (55–26%), while the proportion of trees increases drastically (20–39%). Similarly, the proportion of shrubs increases by 50% from west to east, i.e. from 18.5% to 28% (Table 2). Scatter plots suggest that species richness (number of species) is positively related to the number of forest vegetation types, forest area, and ruggedness index; and negatively related to aridity index (Figure 2). The negative relationship with the aridity index suggests a limiting role of climate on species distribution along India's longest longitudinal extent.

In Poisson GLM analyses, all four predictor variables were statistically significant ($P < 0.001$; Table 3). A decrease in the number of vegetation types resulted in a 42% decrease in the deviance compared with the full model, indicating that this variable contributed the most

to model fit. In comparison, a decrease in RI, FA and AI resulted in a 21.3%, 10.7% and 10.1% reduction in deviance respectively.

We analysed the distribution of plant diversity with respect to climate, topography, vegetation types and disturbance, both single and in combination. The increase in woody tree species from west to east parallels other studies in North America and Italy⁴⁻⁶. The decrease in herbs from east to west could be attributed to the availability of suitable non-summer season in the west and non-availability of sunlight for the ground herbal flora in woody-tree dominant forests in the east. The lower species richness in the west could be due to desert and hyper arid conditions, whereas higher moisture level ($AI < 2$) has led to higher species diversity with more vegetation types in the east (Figure 1 b and c). The eastern region being mountainous has highly rugged terrain¹⁶ (Figure 1 e), and thereby may hold suitable micro-climates for speciation. In contrast, the central Gangetic plains has experienced forest fragmentation and loss due to large-scale agricultural extension and intensification¹⁷ (Figure 1 d); in turn leading to lowering in plant species richness¹⁸.

The present study emphasizes the relevance of four selected predictors in influencing plant diversity along the longitudinal extent. The dominant contribution of the number of vegetation types supports the habitat heterogeneity hypothesis and role of terrain-induced microclimate in explaining the variation in species richness as revealed

Table 3. Coefficient and confidence intervals at 95% confidence level for selected predictor variables under Poisson error distribution model. Results show that all the chosen predictor variables are statistically significant at $P < 0.001$

Predictor variable	Coefficient		Confidence intervals	
	Estimate	Standard error	2.50%	97.50%
(Intercept)	3.9175	0.1168	3.6856	4.1433
Number of vegetation types	0.1039	0.0054	0.0933	0.1146
Forest area	-0.0197	0.0027	-0.0250	-0.0145
Ruggedness index	0.0380	0.0029	0.0323	0.0438
Aridity index	0.0632	0.0088	0.0460	0.0803

from the GLM analysis. Emergence of number of forest vegetation types as the major predictor of species diversity may be explained by the fact that different habitat types have different diversity content. Vegetation types and topography have strong, positive contribution, whereas AI is an inverse predictor. Non-forest area (which includes cultivation, settlements and orchards) revealed the contribution of disturbance as the major concern for plant diversity and its pattern¹⁸. Thus, variation in species richness along the Indian longest longitudinal extent is consistent with some of the hypotheses such as spatial heterogeneity¹⁹, disturbance²⁰ and habitat heterogeneity²¹. This study was enabled by the availability of topology and climate data in the public domain, and plant species data through a national database.

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