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Beta diversity of angiosperms in the tropical forests of Nilgiri Biosphere Reserve, India

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Abstract: The paper aims to evaluate the beta diversity in homogeneous and heterogeneous habitats in tropical forests. Also, the relationship between beta diversity and richness in the rain forests and monsoon forests is elucidated. The study was conducted in a forest landscape of Nilgiri Biosphere Reserve in the Western Ghats of India. The Wilson and Shmida index was used to assess the beta diversity of the angiosperms of the region. Results showed that species richness and beta diversity varied in different vegetation types; in heterogeneous habitats, species turnover was mainly due to habitat restriction, and not dispersal limitation, whereas within a homogeneous habitat beta diversity was dependent on dispersal limitation. Most of the species were restricted to specific habitats; a few species were more adapted to a wide spectrum of climatic conditions. Beta diversity and species richness of rain forests were higher than those of the monsoon forests.

Resumen: El objetivo de este artículo es evaluar la diversidad beta en hábitats homogéneos y heterogéneos en bosques tropicales. Además, se esclarece la relación entre la diversidad beta y la riqueza en los bosques lluviosos y los bosque de monzón. El estudio se llevó a cabo en un paisaje forestal de la Reserva de la Biosfera Nilgiri en los Gates Occidentales de la India. Se usó el índice de Wilson y Shmida para evaluar la diversidad beta de las angiospermas de la región. Los resultados mostraron que la riqueza de especies y la diversidad beta variaron entre los diferentes tipos de vegetación; en los hábitats heterogéneos el recambio de especies se debió principalmente a las restricciones del hábitat y no a la limitación de la dispersión, mientras que en un hábitat homogéneo la diversidad beta dependió más bien de la dispersión limitada. La mayoría de las especies estuvieron restringidas a hábitats específicos y sólo unas pocas especies estuvieron adaptadas a un espectro amplio de condiciones climáticas. La diversidad beta y la riqueza de especies fueron mayores en los bosques lluviosos que en los bosques de monzón.

Resumo: O trabalho tem como objetivo avaliar a diversidade beta em habitats homogéneos e heterogéneos em florestas tropicais. Além disso, elucida-se a relação entre a diversidade beta e riqueza nas florestas tropicais e florestas de monção. O estudo foi conduzido numa paisagem florestal da Reserva da Biosfera de Nilgiri nos Ghats ocidentais da Índia. O índice de Wilson e Shmida foi usado para avaliar a diversidade beta das angiospérmicas da região. Os resultados mostraram que a riqueza de espécies e diversidade beta variou em diferentes tipos de vegetação; em habitats heterogéneos, o volume de espécies deveu-se principalmente à restrição do habitat, e não à limitação da dispersão, enquanto que num habitat homogéneo a diversidade beta era dependente da limitação da dispersão. A maioria das espécies estavam restritas a habitats específicos; algumas espécies estavam mais adaptados a um amplo espectro de condições climáticas. A diversidade Beta e a riqueza de espécies das florestas tropicais foram superiores aos das florestas de monção.

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Key words: Beta diversity, ecological amplitude, monsoon forests, rain forests, tropical forests, Western Ghats.

Introduction

Spatial patterns of species diversity change over multiple spatial scales. The pattern observed within a local community may be very different from those found over broader areas such as landscapes or regions (Willis & Whittaker 2002). The terms "beta diversity" and "species turnover" are often used interchangeably in ecological literature (Harrison *et al.* 1992). In the present study, the concepts as defined by Vellend (2001) are used. According to him, "beta diversity" expresses the relationship between the total number of species in a set of study plots and average number of individuals, and "species turnover" is defined as the rate or magnitude of change in species composition along predefined spatial or environmental gradients. To him, "beta diversity" and "species turnover" are numerically equivalent, the difference being simply that "beta diversity" compares samples within a community, "species turnover" samples from different communities. Beta diversity has been the focus of theories relating species richness and the species-area function to habitat and distance (Arita & Rodriguez 2002; Balvanera *et al.* 2002; Tuomisto *et al.* 2003). Spatial separation of landscapes within a region could maintain beta diversity through dispersal limitation, and produce a pattern of 'distance decay of similarity' (Nekola & Kraft 2002). Several factors influencing species turnover have been recognized including those related to the environment and its heterogeneity, and those inherent to the species, like its dispersal ability and levels of tolerance to different environmental factors.

Environmental heterogeneity in the form of spatial variation in habitat and local climate can affect species distribution and hence beta diversity. This assumes that heterogeneous habitats may provide more niches and diverse ways of exploiting the environmental resources, and thus increase species diversity (Bazzaz 1975; Simpson 1949). Study of species turnover in relation to distance and climate differences addresses the contribution of historical and geographic factors relative to that of the contemporary environment in evolving patterns of species richness (Dufour *et al.* 2006; Latham & Ricklesfs 1993). Most theories explaining the high diversity of tropical tree species rely on the effects of habitat and distance (Soininen *et al.* 2007). Niche-assembly theories (Clark *et al.* 1998) stress the importance of environmental heterogeneity, while dispersal-assembly theories (Hubbel *et al.* 1999) emphasise the effects of spatial isolation, together with dispersal limitation. Disentangling the effects of habitat differences versus geographic distance is essential in understanding the basis of the high turnover of tree species which is observed in the tropics.

There are few studies on beta diversity at different scales ranging from local communities to ecoregions (Brown 2001; Mena & Vazquez-Dominguez 2005; Qian *et al.* 2009). Most beta-diversity studies in the tropics were carried out in the Amazonian basin or in Central America (Pitman *et al.* 2001; Tuomisto *et al.* 2003), and few attempts have been made to examine the influence of environmental factors on species assemblages in tropical forests at a regional scale. Recently, in the evergreen forests of the Western Ghats, Davidar *et al.* (2007) related the rate of turnover of trees with distance to latitude, rainfall gradient and seasonality. The present study analyses beta diversity of angiosperms in the forest landscape of the Nilgiri Biosphere Reserve (NBR) in the Western Ghats of India, which harbour all the major vegetation types of the region. This mountain range in peninsular India extends to a length of more than 1400 km, and is recognized as one of the 34 hotspots of biodiversity in the world, rich in both floral and faunal elements, including endemics (Weblink 2007). The western slopes of the Ghats receive heavy rainfall, ranging from 2000 to 6000 mm per annum. But in the hill ranges towards the East, the rainfall decreases and the slopes and foothills of the Ghats here are almost rain-shadow areas. The New Amarambalam Reserve forests of the NBR are one of the richest parts of the Western Ghats from the biodiversity point of view, harbouring several endemics, and species at risk of extinction (Jayakumar & Nair 2005; Nair & Jayakumar 2005, 2008).

It has been known that the proportion of rare species or species with restricted distribution strongly influences beta diversity (Routledge 1977). In the present study, changes in the species composition of angiosperms across a tropical forest landscape in the Nilgiri Biosphere Reserve were investigated. Here species turnover along two transects (the "cross-community" transect passing through many vegetation types with a high proportion of rare and endemic species restricted in distribution, and the "within-community" transect, in a single vegetation type with a high proportion of widely distributed species) was investigated. Also, species with higher ecological amplitude[1] in the forest landscape and their role in species turnover were identified and assessed. The study aimed to test the hypothesis that increased environmental heterogeneity enhances the beta diversity and richness of the plant communities. Based on this hypothesis, the following questions addressed here are: Is beta diversity and species richness of rain forests higher than those of monsoon forests? Is there any difference in the beta diversity of trees in homogeneous and heterogeneous habitats (as exemplified by the two transects)? Do species show restriction in distribution to specific habitats? Is there any direct relationship between the ecological amplitude of species and beta diversity? The present study reveals that these forest landscapes, especially the rain forests, have high beta diversity, high species richness and a large number of rare and endemic species restricted to different habitats. Such a forest landscape requires special care for its biodiversity and for the conservation of the species making it up.

Methods

Study area

The study area, namely the New Amarambalam Reserve Forests, forms part of the core area of the Nilgiri Biosphere Reserve, situated along the western slope of the Western Ghats of India, within Kerala State (see map, Fig. 1). The area covers about 265 km^2 between 11° 14' and 11° 24' N latitude and between 76° 11' and 76° 33' E longitude. The natural vegetation types of the area are tropical moist deciduous forests (MOIS), tropical semievergreen forests (SEMI), tropical evergreen forests (EVER), subtropical broad leaved hill forests (SUBT), subtropical savannas (SAVA), montane wet temperate forests (MONT) and montane wet temperate grasslands (GRAS) (Champion & Seth 1968). Of the seven vegetation types, moist deciduous forests - a monsoon forest exclusively dependent on seasonal monsoon rain - are situated in the foothills of the Ghats, while the other forest formations are at higher elevations, and are mainly rain forests (receiving rain throughout the year because of the topography). These vegetation types are located at altitudinal ranges between 40 m and 2600 m above msl. The lowest region of the Ghats is dominated by moist deciduous forests in an altitudinal range of 40 - 400 m. As elevation increases, the vegetation types change to tropical semievergreen forests (400 - 650 m), tropical evergreen forests (650 - 1200 m), subtropical savannas (1000 - 1500 m), subtropical hill forests (1200 - 1800 m) and montane temperate forests (1800 - 2500 m); the topmost formation being the montane temperate grasslands occupying an elevation of 1800 - 2600 m. Among the seven vegetation types, subtropical savannas and montane temperate grasslands are dominated by grasses as a result of frequent fire during summer caused by anthropogenic disturbance. Temperatures in the area range from 17 to 37 °C, and the diurnal variation never exceeds 16 °C. The average rainfall is above 2600 mm, and sometimes in the hills may reach up to 6000 mm. Most of the precipitation is during the south-west monsoon, which starts in June and lasts till the end of September. In addition, at the high altitudes of the Ghats, topographic factors lead to rain being received throughout the year. The monsoon precipitation is maximum on hill slopes with western, south - western and north - western aspects.

Vegetation sampling and analysis

Vegetation analysis was conducted during the years 1998 - 2003. Forty-six sample areas, each of one hectare, were defined (see map, Fig. 1) Sixteen of these were located at two-kilometre intervals along each of two transects, one roughly following the contours within tropical moist deciduous forest (the "within-community" transect), the other crossing the contours and thus taking in all four main vegetation types (the "cross-community" transect). To increase understanding

[1] Ecological amplitude is the capacity of a species to establish in various habitats lying along an environmental gradient (Varghese & Menon 1999).

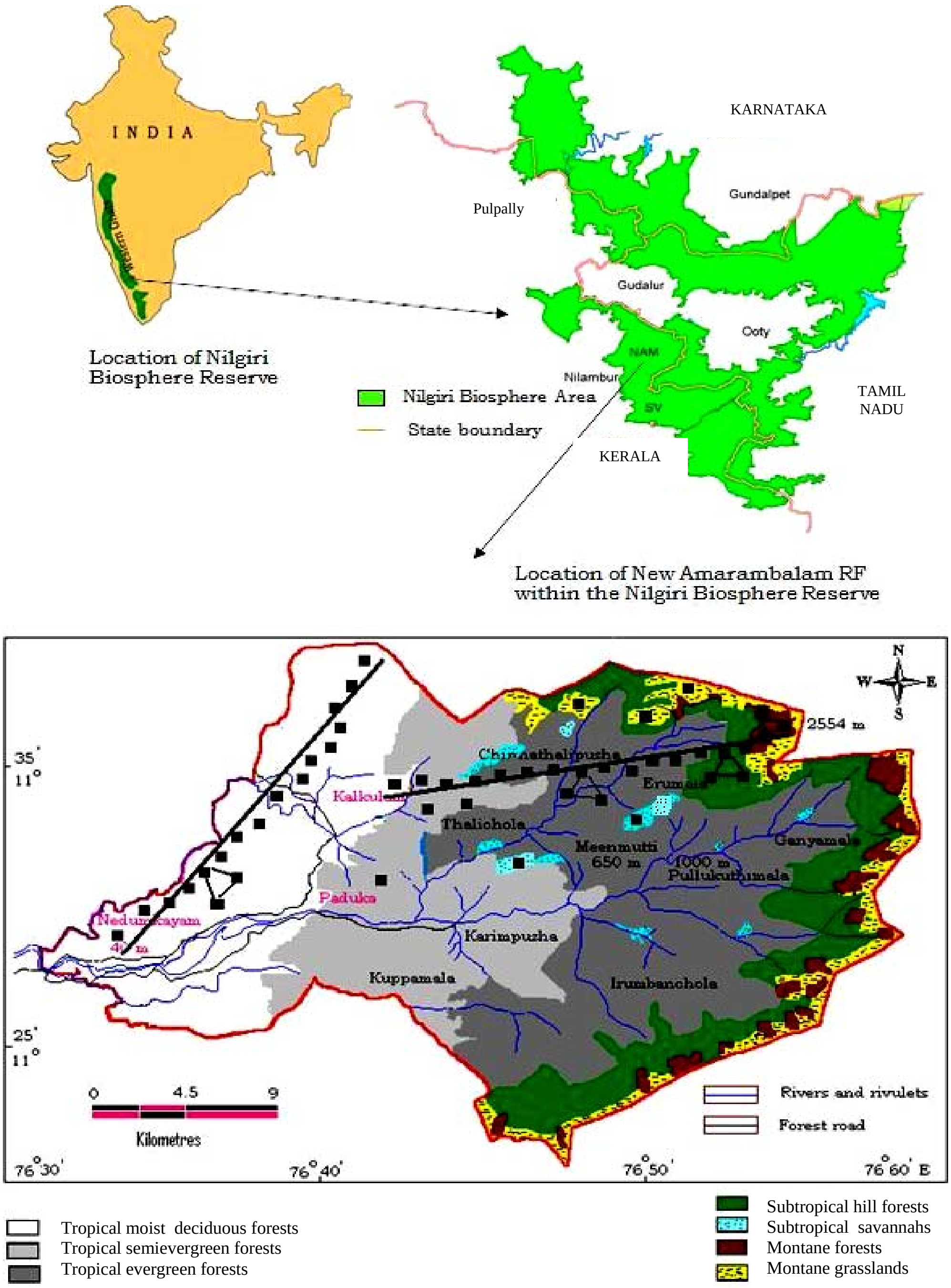

Fig. 1. Map of the study area, showing different vegetation types and location of sample areas.

of variation within a vegetation type, four additional pairs of sample areas were located, each pair forming an equilateral triangle (with side 3 km) with one of the sample areas on a transect. Since some of the vegetation types were not included in this sampling programme, six additional sample areas were selected to cover them (see map, Fig. 1). The exact location of the sample areas was subject to conditions such as accessibility and the nature of the terrain. Each of the sample areas was divided into eleven quadrats 30 m x 30 m, within which all the standing trees (> 10 cm gbh) were recorded. Within each quadrat, ten random sub-plots 5 m x 5 m were designated for recording shrubs, and ten independent random sub-plots 2 m x 2 m for recording herbs. In each category, only angiosperms were recorded. To assess the dominance status of species in each of

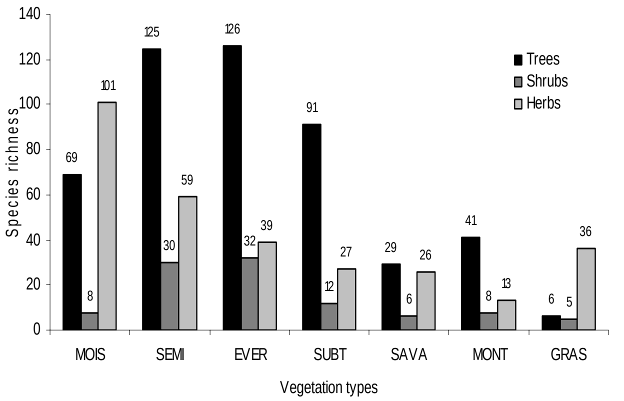

Fig. 2. Species richness of different life forms in the different vegetation types* of the study site. Species richness is high in medium-elevation forests like semievergreen forests and evergreen forests.
*MOIS - tropical moist deciduous forests; SEMI - tropical semievergreen forests; EVER - tropical evergreen forests; SUBT - subtropical hill forests; SAVA - subtropical hill savannahs; MONT - montane wet temperate forests; GRAS - montane wet temperate grasslands.

the vegetation types, density (number of individuals ha^{-1}) of each species was calculated.

To assess between-habitat species turnover, for each vegetation type a random set of quadrats was selected proportional in number to the area of that vegetation type within the 265 km^2 studied, from 23 for subtropical savannahs to 78 for tropical evergreen forests.

To study the beta diversity of angiosperms within a habitat, four vegetation types were selected at different altitudinal ranges, viz. moist deciduous forests (monsoon forests), evergreen forests, subtropical hill forests (medium elevation rain forests) and montane forests (high elevation rain forests). For this analysis, the triangular arrays of sampling areas mentioned above (Fig. 1) were used.

The two transects described were used to study the beta diversity of trees within homogeneous vegetation (the "within-community" transect, covering an elevation range from 40 to 300 m) and the species turnover in heterogeneous habitats (the "cross-community" transect; covering an elevation range from 100 to 2400 m).

In order to measure changes in species composition between site or habitat pairs (beta diversity or species turnover), the formula of Wilson & Shmida (1984) was used:

$$ß = (b + c) / (2a + b + c),$$

where, ß = beta diversity (or species turnover), a = total number of species that occur in both sites, b and c = number of species that occur in one or the other site only. The Pearson correlation was used to test the correlation between beta diversity and species richness in different vegetation types. The Mann-Whitney *U*-test was used to compare beta diversity along the two transects using the statistical package *SPSS* (Version 16). A paired *t*-test was conducted to determine the amount of variation in species richness and density along the two transects.

Results

Species richness

A total of 526 species of angiosperms including 242 trees, 59 shrubs and 225 herbs were recorded from the sampled area. The highest species richness was in the semievergreen (214 species) and evergreen (197) forests, and it was least in fire-affected formations like subtropical savannas (61) and montane grasslands (47), located along the crest of the mountain ridge. Semievergreen forest is a transitional forest formation with a higher content of trees, a substantial content of shrubs and herbs, and the highest overall species richness (Fig. 2). Most species were trees except in the savannas and montane grasslands, where grasses are the dominant life form, and in monsoon forests (moist deciduous forests) where the richness of herbs was very high and trees were less speciose than in rain forests. The species richness of herbs in the monsoon forests was higher than in rain forests.

Beta diversity and species turnover

Species turnover of angiosperms between different vegetation types ranged from 0.40 to 1.00; most of the lower turnover values were recorded between neighbouring vegetation-type pairs (Table 1). The angiosperms in the moist deciduous forests showed 69 per cent turnover with adjacent semievergreen forests. The lowest turnover (ß = 0.40) was between evergreen forests and semievergreen forests, which shared 111 angiosperm species. On the other hand, between semi-evergreen forests and montane grasslands, which shared no species, the species turnover was cent percent (ß = 1). Fire-affected and grass-dominated vegetation types such as subtropical savannas and montane grasslands have higher turnover with adjacent tree - dominated vegetation types - for

Table 1. Beta diversity between-habitats (below diagonal) and number of angiosperm species shared (above diagonal) among vegetation types. Species turnover in the adjacent forest pairs is lower than distant forest pairs.

Vegetation types*	MOIS	SEMI	EVER	SUBT	SAVA	MONT	GRAS
MOIS		52	29	10	12	2	1
SEMI	0.69		111	51	15	4	0
EVER	0.84	0.40		90	21	10	1
SUBT	0.93	0.70	0.51		20	19	4
SAVA	0.88	0.89	0.85	0.79		6	5
MONT	0.98	0.98	0.93	0.81	0.89		14
GRAS	0.99	1.00	0.99	0.96	0.91	0.73	

*MOIS - tropical moist deciduous forests; SEMI - tropical semievergreen forests; EVER - tropical evergreen forests; SUBT - subtropical hill forests; SAVA - subtropical hill savannahs; MONT - montane wet temperate forests; GRAS - montane wet temperate grasslands.

Table 2. Beta diversity of angiosperms (within-habitat) was higher in the rain forests than in monsoon forests. Species richness of trees and shrubs in the rain forests is higher than those in monsoon forests, where richness of herbs was higher. The altitudes and species richness of each vegetation type are given in brackets.

Vegetation types (Altitudes)	Beta diversity (mean ± SD; n = 3) (Species richness)		
	Trees	Shrubs	Herbs
Monsoon forests			
Tropical moist deciduous forests (40-300 m)	0.10 ± 0.04 (42)	0.21 ± 0.03 (6)	0.15 ± 0.05 (73)
Rain forests			
Tropical evergreen forests (800-1000 m)	0.28 ± 0.04 (75)	0.31 ± 0.06 (15)	0.36 ± 0.05 (25)
Subtropical hill forests (1400-1600 m)	0.26 ± 0.01 (81)	0.35 ± .03 (10)	0.37 ± 0.06 (21)
Montane temperate forests (2000-2300 m)	0.17 ± 0.06 (41)	0.27 ± 0.05 (8)	0.32 ± 0.05 (13)

instance subtropical hill forests and subtropical savannas (SUBT-SAVA, ß = 0.79), subtropical savannas and evergreen forests (SAVA-EVER, ß = 0.85) and montane temperate forests and montane temperate grasslands (MONT-GRAS, ß = 0.73) showed high turnover even though they were adjacent. Almost complete replacement of species occurred in distant habitat pairs such as moist deciduous forests and montane temperate grasslands (MOIS-GRAS, ß = 0.99), evergreen forests and montane grasslands (EVER-GRAS, ß = 0.99) and subtropical hill forest and montane temperate grasslands (SUBT-GRAS, ß = 0.96) (Table 1). Also, moist deciduous forests and montane temperate forests shared only two species, namely *Macaranga peltata* and *Persea macrantha.* The montane temperate forests shared only a single species, viz. *Macaranga peltata,* with the moist deciduous and evergreen forests found at lower elevations.

At the local scale, beta diversity of all life forms, except herbs, was higher in the rain forests (evergreen, subtropical and montane forests) than in monsoon forests (moist deciduous forests). Beta diversity within a vegetation type was higher in the forests at intermediate elevation (800 - 1600 m) than in those on the foothills or on top of the mountains (Table 2). In both rain and monsoon forests, beta diversity of trees (0.10 to 0.28) were lower than those of shrubs (0.21 to 0.35) and herbs (0.15 to 0.37) even though species richness of these forest types varies. The correlation between beta diversity and species richness among sampled sites of different vegetation types was moderately high (trees: r = 0.861, P = 0.139; shrubs: r = 0.909, P = 0.081; herbs: r = -0.908, P = 0.092). Correlation was negative in the case of herbs while it was positive for trees and shrubs over all the vegetation types. Species richness of trees and shrubs in the rain forests was higher than in monsoon forests, where richness of herbs was greater.

Species turnover rate was higher for a distance of about 30 km along the “cross-community” transect as compared to the “within-community” transect. In the “within-community” transect, species turnover increased gradually with distance, and at 30 km the turnover was 44 per cent. But, in the cross-community transect, rapid increase persisted to 26 km and at this distance, the turnover was 100 per cent at an elevation of 1800 m (Fig. 3). Species richness and density were higher in the flora along the cross-community transect (183 and 415) than the within-community transect (79 and 149; P < 0.0001; Table 3). Using the Mann-Whitney U-test, the species turnover of

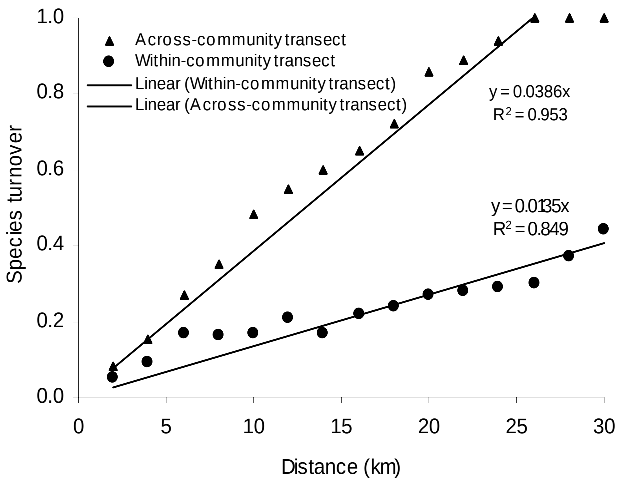

Fig. 3. Scatter-plot analysis indicating the species turnover (or beta diversity) of trees with distance along the “within-community” and “cross-community” transects.

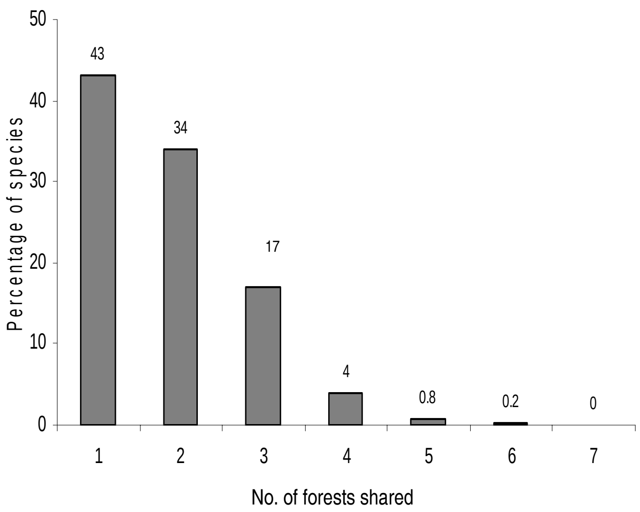

Fig. 4. Percentage of taxa shared between different forest types. These figures show that most of the taxa are adapted to one or two habitats only, and species with wide ecological amplitude are few.

tree species along the “cross-community” transect (R^2 = 0.953) and the “within-community” transect (R^2 = 0.849) were compared. Results indicate a significant difference (P < 0.001) in the species turnover along the two transects.

Ecological amplitude of species and their endemism

In the study area, 43 per cent of the taxa were restricted to a single vegetation type, while only 0.2 per cent of the taxa shared six vegetation types

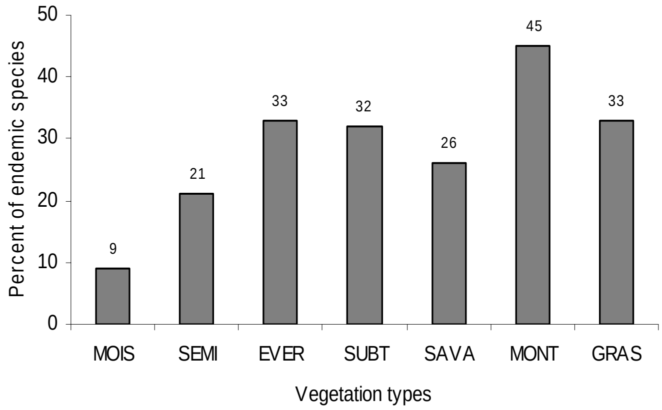

Fig. 5. Distribution of endemic species between different vegetation types of the study area. Endemic species are more numerous in rain forests than in monsoon forests (moist deciduous forests).

(Fig. 4). Considering as “dominant” those species which were among the three with highest density in a particular stratum in a vegetation type, a total of 53 species of angiosperms were recorded as dominant in one or other of the seven vegetation types (see Appendix Table 1). Habitat preferences of several species were also evident, with 223 species found in only one of the seven vegetation types. A total of 21 species (e.g. *Breynia retusa, Cassia fistula, Cyrtococcum oxyphyllum* and *Strobilanthes ciliatus*) shared four vegetation types, and only four species (*Acronychia pedunculata, Chromalaena odorata, Clerodendrum viscosum* and *Persea macrantha*) shared five. *Macaranga peltata,* a secondary species, was the only taxon recorded in almost all the vegetation types of the landscape, except the montane grasslands. A total of 114 species endemic to the Western Ghats were recorded from the study area and most of them were restricted to rain forests (Fig. 5); in monsoon forests, exotic species were more numerous, and here the density of most of the endemic species was comparatively lower than other species.

Discussion

Species richness is a fundamental measure of community and regional diversity. Among the total flora, trees constitute the life form with the greatest number of species (46 %), followed by herbs (43 %) and shrubs (11 %). Moist deciduous forests receive only monsoon showers, and overall species richness in this vegetation type is lower than in rain forests. But the species richness of herbaceous flora in moist deciduous forests was higher than in

Table 3. A comparison of species richness, density, range of turnover and other topographic and climatic parameters of tree species in homogeneous (within-community) and heterogeneous habitats (across communities) along the 30 km transects. There is a significant difference in species turnover (using Mann-Whitney *U*-test) and community structure (paired *t*-test) of trees in homogeneous and heterogeneous habitat.

Variables	Transects		*P*-value
	within-community	across-communities	
Sampled area (ha)	15	15	
Range of turnover	0.05 - 0.44	0.08 - 1.00	0.001
Species richness	79	183	
Density (individuals ha^{-1})	149	415	0.0001
Altitude range (m)	40 - 300	40 - 2400	
Rainfall range (mm)	1500 - 2500	3000 - 6000	
Slope range (%)	0 - 10	10 - 75	

other vegetation types. On the other hand, other vegetation types in the upper ghats (i.e. rain forests) receive seasonal monsoon rainfall as well as regular rains. Maximum species richness occurred in semievergreen forests, which is a transition forest zone between monsoon forests and rain forests. Montane grasslands and savannas are grass-dominated as a result of regular forest fire; repeated burning promotes the establishment of fire-tolerant species, while it prevents colonization by trees by damaging their seedlings.

Adjacent vegetation types have lower species turnover than distant ones, except for the fire-affected and grass-dominated types, which showed very high species turnover when compared with the adjacent vegetation types. In natural forests, there is no barrier between adjacent vegetation types and most of the new recruits grow close to their parent plants. Limitation in dispersal can also alter the beta diversity comparisons among different life forms (Nekola & White 1999). In comparing different vegetation types, the lower level of beta diversity for trees as compared to shrubs and herbs suggests that the latter two life forms are more restricted in dispersal, and that trees have a wider range. At the local scale, beta diversity of monsoon forests is lower than most of the rain forest types, because of the high species richness of the latter. Increased species richness enhances the potential for dispersal limitation (i.e. lack of propagules to colonize suitable habitats) and thus promotes neutrality in Hubbell's sense (Hubbell 2001; see also Gravel *et al*. 2006)

High beta diversity is also associated with a narrow range of distribution for many species which results in small local populations. The higher value of beta diversity observed at mid-elevations of 800 - 1600 m can be linked to distribution of plants along the altitudinal gradient. Also, the undulating terrain of these areas promotes the formation of many different microclimatic conditions, and such regions have optimum climatic conditions for better survival of plants. Low species turnover at higher elevations reflects the co-occurrence of species in those elevational ranges. According to Steven's rule (Steven 1992), at higher elevations there is an increase in the elevational range of species, and this can increase the probability of overlap between species ranges. Thus, it can be inferred that turnover decreases at higher elevations, as a result of the presence of species with larger elevational ranges.

The study also showed that beta diversity at the level of sampling area (1 ha) increased with increasing distance among different sampling areas in the mountain range. The greater amount of variation in species turnover, as observed in the "cross-community" transect, reflects the niche effect on species distribution. This rapid turnover of tree species along the "cross-community" transect is due to change of habitats over a short distance. Species turnover had higher values as the elevation differences became larger. In the study area, a heterogeneous habitat (steeper topographical gradient) led to more species richness and greater species turnover than a homogeneous habitat (more gradual gradient). This is similar to what has been described for Neotropical forests, where a higher turnover in a Panamanian plot has been partly attributed to greater variations in topography (Condit *et al.* 2002). Neutral theory (Hubbel 2001) predicts that similarity decay happens in environmentally homogeneous landscapes and the decay curve will be smooth, depending on the dispersal rate. On the other hand, under niche assembly theory (Gaston & Chown 2005), similarity decay results from species turnover along gradients of environment or habitat, and the associated similarity decay will not be smooth because of typically patchy and recurrent habitats with sharp boundaries.

In plants, dispersal of propagules is effected by various agents, and the mere carrying of propagules to new areas will not ensure their germination and growth, unless there are suitable climatic and edaphic conditions there. Interaction of each species with the biotic and abiotic environment determines whether it will flourish in a particular habitat. Propagules of the majority of trees in the monsoon forests cannot easily grow in very rich rain forests with a closed canopy, continuous rainfall and high humidity (Jones 1983). Restriction of species to a particular habitat increases beta diversity at the regional scale. In the study area, most of the endemic species are restricted to rain forests, and many endemics have lower abundance as compared to their more cosmopolitan relatives. Monsoon forests are situated in the foothills of the Ghat near to human habitation, and, as MacDonald *et al.* (1989) reported, an increase in the number of human visitors to an area leads to an increase in the number of exotic species. The majority of the species, especially endemics, were restricted to either one or two forest types, and few species were adapted to different climatic conditions. Several researchers have reported significant species-habitat associations for only a limited number of specialised species, and thus argue that history and local dispersal mechanisms may be the major processes underlying differences in the spatial distribution patterns of tropical tree species (Bitman *et al.* 2003; Harms *et al.* 2001). Species with high ecological amplitude cause a decrease in species turnover on account of their dispersal ability (Munzbergova & Herben 2005) and tolerance of different climatic conditions. Another important observation during the study is that no species with high ecological amplitude is dominant in any of the vegetation types except for the invasive weed *Chromalaena odorata* (see Appendix Table 1).

In conclusion, each vegetation type in this part of the tropics is distinct from the others in relation to species richness and composition. Beta diversity of angiosperms in the rain forests is higher than in monsoon forests. In heterogeneous habitats, species turnover is mainly due to habitat restriction rather than dispersal limitation; in homogeneous habitat, it is mainly dependent on dispersal limitation. A substantial number of species are restricted to a particular habitat; species with lower ecological amplitude increase beta diversity, while those with higher ecological amplitude decrease beta diversity. Therefore, the study shows that suitability of habitat, limitations in dispersal, and ecological amplitude are important aspects contributing to the beta diversity of plant species in the tropics.

Relevance and implications for conservation

The important aspects of the spatial organization of diversity in this landscape in relation to conservation are the high variation in species composition among habitats, and the concentration of endemic species in rain forests. High species turnover along an environmental gradient reflects habitat specialization by the constituent species, and quantifying species turnover along such gradients can facilitate the evolution of strategies for protecting the biological diversity of a landscape. Spatial variation in species composition within a habitat type is important in identifying areas for the protection of species of that habitat type. The specialization that creates high beta diversity also exposes species to risk in the face of climatic shifts, which can drive species up-slope and reorganize communities. Many species, especially endemics in the study area, are limited to a particular habitat, so that predicted changes in climatic factors would be sufficient to cause local extinction, although biological interactions would also probably influence such range extinctions. High species turnover calls for greater care in the management of a reserve, particularly in deciding its pattern and extent in a heterogeneous landscape, as compared to certain lowland monsoon forests.

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Appendix Table 1. Density (mean individuals per hectare) of dominant angiosperm species (first three of each life-form) in various forest types and their distribution in other vegetation types of the study area; '+' represents the presence of the species. The sampled area of each forest type is also given.

Species	Density (mean ind. ha^{-1})						
	MOIS	SEMI	EVER	SUBT	SAVA	MONT	GRAS
Trees (≥ 10 cm gbh)							
Xylia xylocarpa	25.9	+	-	-	-	-	-
Terminalia paniculata	22.8	+	+	-	-	-	-
Lagerstroemia microcarpa	15.6	+	+	-	-	-	-
Pterygota alata	-	51.1	+	-	-	-	-
Reinwardtiodendron anamalaiense	-	28.1	+	-	-	-	-
Strombosia zeylanica	-	14.3	-	-	-	-	-
Palaquium ellipticum	-	+	99.4	55.2	-	-	-
Agrostistachys borneensis	-	+	76.9	+	-	-	-
Myristica beddomei	-	+	43.4	90.2	-	-	-
Litsea stocksii	-	-	+	32.7	-	-	-
Wendlandia thyrsiflora	-	-	-	-	15.1	-	-
Phyllanthus emblica	+	-	-	-	3.2	-	-
Glochidion neilgherrensis	-	-	-	-	2.3	+	-
Turpinia cochinchinensis	-	-	-	+	-	105.9	-
Rhododendron arboretum	-	-	-	+	-	102.5	-
Symplocos obtusa	-	-	-	-	-	64.1	-

Contd...

Appendix Table 1. Continued.

Species	Density (mean ind. ha^{-1})						
	MOIS	SEMI	EVER	SUBT	SAVA	MONT	GRAS
Shrubs							
Chromalaena odorata	826	+	+	-	120		-
Helicteres isora	304	+	-	-	-		-
Glycosmis pentaphylla	78	+	-	-	-		-
Strobilanthes heyneanus	-	333	+	+	-		-
Strobilanthes amabilis	-	177	+	+	-		-
Thottea siliquosa	-	118	447	+	-		-
Elatostemma lineolatum	-	-	176	-	-		-
Psychotria anamallayana	-	+	167	-	-		-
Strobilanthes luridus	-	-	-	555	-	600	64
Strobilanthes sp.	-	-	-	275	-	1114	-
Strobilanthes barbatus	-	+	+	240	-	-	-
Clerodendrun serratum	-	+	-	-	40	-	-
Lobelia nicotianifolia	-	-	-	-	40	-	-
Lasianthus acuminatus	-	-	-	-	-	414	-
Gaultheria fragrantissima	-	-	-	-	-	-	93
Ixora cuneifolia	-	-	-	-	-	-	85
Herbs							
Sacciolepis indica	243132	-	-	-	-	-	-
Urena lobata	13137	+	-	-	+	-	-
Isachne globosa	23921	-	4392	-	+	-	-
Pellionia heyneana	-	7454	-	-	-	-	-
Oplismenus compositus	-	7090	-	-	-	-	-
Garnotia tenella	-	5272	2803	-	-	-	-
Peliosanthes teta	-	+			-	-	-
Zingiber zerumbet	-	+		+	-	-	-
Impatiens cordata	-	-		3291	-	+	-
Pouzolzia indica	-	-	1308	2658	-	-	-
Carex raphidocarpa	-	-		1518	45000	-	-
Chrysopogon hackeli	-	-	+	-	18666	-	-
Themeda triandra	-	-	-	-	4000	-	-
Cassia kleinii	-	-	-	-	+	-	-
Impatiens goughi	-	-	-	-	-	10000	+
Impatiens leshenaultii	-	-	-	-	-	5000	+
Arundinella leptochloa	-	-	-	-	-	3500	+
Arundinella purpurea	-	-	-	-	-	+	92500
Eulalia phaeothrix	-	-	-	-	-	-	33000
Cyperus wightiana	-	-	-	-	-	-	17000
Sampled area (ha)	4	5	7	5	2	3	2