RESEARCH PAPER

The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees

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ABSTRACT

Aim We assessed the rates of turnover of tree species with distance (beta diversity) in wet forests of the Western Ghats (WG) complex of India to see whether climate, topographic variation or species traits influence beta diversity.

Location The Western Ghats is a chain of mountains about 1600 km in length, running parallel to the western coast of the Indian Peninsula from above 8° N to almost 21° N latitude.

Methods We used data from 60 small plot inventories concentrated in three regions: the southernmost part of the Western Ghats (SWG) (8°24′ to 9°37′ N), the Nilgiri Hills (11°12′ to 11°14′ N), and the central Western Ghats (CWG) (12°32′ to 14°51′ N). We used Sorensen's index (SI) to estimate the similarity in species composition between two plots and regressed SI against the logarithm of the distance between plots to assess beta diversity. A bootstrapping procedure provided confidence intervals for regression coefficients. To test for the effects of climate, we regressed seasonality differences between plots against SI for low-elevation (< 800 m) plots along the north–south axis, and all plots in the SWG. We assessed the impact of the rainfall gradient in the Kogar region.

Results Among all three regions, beta diversity was highest along the latitudinal axis, and along the rainfall gradient in the Kogar region. Differences in seasonality between sites were strongly related to beta diversity along the north–south seasonality gradient and within the SWG. Within the three regions, beta diversity was highest in the region with the strongest rainfall gradient and lowest for the topographically heterogeneous SWG. Beta diversity did not differ between forest strata and dispersal modes.

Main conclusions We conclude that climate, particularly seasonality, is probably the primary driver of beta diversity among rain forest trees of the Western Ghats complex.

Keywords

Beta diversity, climatic gradient, India, latitudinal gradient, topographic heterogeneity, trees, tropical rain forest, Western Ghats.

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INTRODUCTION

Similarity in plant species composition decreases with increased distance between census plots. The mechanisms that regulate this species turnover, or beta diversity, are difficult to demonstrate. Beta diversity can be influenced by several factors, such as differences in climate, soil or topography and dispersal limitation (Nekola & White, 1999; Bell, 2001; Condit *et al.*, 2002; Tuomisto *et al.*, 2003; Leigh *et al.*, 2004). The comparison of beta diversity among regions with different climate and topography could provide insights into regulatory processes. The role of neutral processes such as dispersal limitation is more difficult to evaluate.

Comparative studies have shown that beta diversity is higher in some plant groups than others (Nekola & White, 1999). In the

spruce–fir forests of North America, species turnover per unit distance was higher for vascular plants than for bryophytes, for animal-dispersed species than for species with wind-dispersed seeds or airborne spores, and for herbs than for woody plants. These differences could be caused by dispersal limitation, since species turnover was greater for smaller than for larger plants and for plants with seeds dispersed by birds and mammals than for plants with wind-dispersed seeds (Nekola & White, 1999). However, a study of beta diversity in 15 taxa, including plants, vertebrates and invertebrates, along the north–south and west–east axes in Britain, showed that dispersal limitation was less important than habitat and range restrictions in influencing beta diversity (Harrison *et al.*, 1992). Dispersal limitation could be more important at local and regional scales.

Annual rainfall and its seasonality are important determinants of plant species richness and diversity in the tropics (Gentry, 1988; Clinebell *et al.*, 1995; Givnish, 1999; Leigh, 1999; Leigh *et al.*, 2004; Davidar *et al.*, 2005) because dry season drought is an important constraint for many tropical plants, particularly species with shallow roots such as shrubs and understorey treelets (Wright, 1992; Condit *et al.*, 1995; Engelbrecht & Kursar, 2003). For example, the alpha diversity of trees declined with increasing seasonality across a latitudinal gradient in rain forests of the Western Ghats (WG), a mountain chain running parallel to the western coast of the Indian Peninsula (Davidar *et al.*, 2005). The extent to which climatic differences influence beta diversity needs to be understood. In the Neotropics, beta diversity was higher along a rainfall gradient in Panama than in regions of western Amazonia with more uniform climate and soil (Condit *et al.*, 2002).

Patterns of beta diversity are also scale dependent. Among British birds, for example, species turnover at small spatial scales was statistically unrelated to turnover at the macroscale (Lennon *et al.*, 2001), and no major effect was decisive at all scales of observation (Whittaker *et al.*, 2001). At the macroscale, predictable variation in annual rainfall and seasonality has important influences on plant species richness (O'Brien *et al.*, 2000), and possibly on beta diversity. Pest pressure could explain the patterns of species diversity at both local and macroscales in rain forests if pest pressure is higher for wetter and less seasonal sites, allowing more species to coexist (Janzen, 1970; Wright, 1992; Givnish, 1999). Davidar *et al.* (2005) showed that tree dominance increased with seasonality in the WG rain forests, as if pest pressure were lower in more seasonal sites.

We predict that if dispersal limitation influences beta diversity, then beta diversity would differ between forest strata and dispersal modes, with the more dispersal-limited categories displaying higher rates of beta diversity. We predict that if climate controls beta diversity rates, then beta diversity would be high along strong rainfall and seasonality gradients, whereas if topographic variation controls beta diversity, then beta diversity would be higher in regions with greater variation in topography. In this study we tested these predictions by comparing the beta diversity of trees of the Western Ghats across climatic gradients, between regions with dissimilar topography and among species occupying different forest strata and differing in dispersal modes.
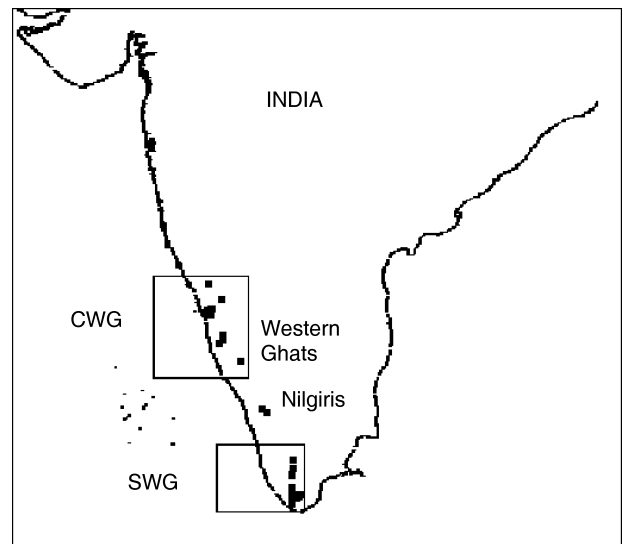

Figure 1 Map of the study area showing the location of plots: CWG, central Western Ghats; SWG, southern Western Ghats.

METHODS

Study area

The Western Ghats (WG) is a chain of mountains about 1600 km in length, running parallel to the western coast of the Indian Peninsula from about 8° N to almost 21° N latitude (Fig. 1). The Nilgiri Hills lie off the WG and form a link to the Eastern Ghats, a range of lower hills on the eastern side of the Indian Peninsula.

The rain forests of the WG occur as a narrow belt from about 8°20′ N to over 16° N latitude, in regions with heavy rainfall. The length of the dry season varies along the latitudinal axis, with the southern sites experiencing a shorter dry season. There are also regional rainfall gradients that vary with the direction of the monsoon winds (Garrigues, 1999). These partially independent rainfall gradients allow us to evaluate the importance of rainfall and seasonality gradients on the beta diversity of trees. Ever-wet forest spans a greater range of elevations in the southern portion of the WG than in the central or northern sections, whereas in the central WG annual rainfall changes within short distances along the direction of the monsoon winds (Garrigues, 1999).

We assessed beta diversity using data from 60 small plots where all trees ≥ 3.18 cm d.b.h. (diameter at breast height, at 1.3 m above the ground) were identified and recorded. These plots were concentrated in three regions: the southern WG (8°20′ N to 10°30′ N), the central WG (12°10′ N to 15° N), and the Nilgiri Hills (around 11° N). Davidar *et al.* (2005) provide the location, dimensions, elevation, rainfall and seasonality for 37 southern WG and central WG plots and Attapadi, which is south of the Nilgiris (Davidar *et al.*, 2005).

The southern Western Ghats (SWG) is an important centre for plant diversity and endemism (Ramesh *et al.*, 1997). Many of the low-elevation wet forests along the western slopes have been degraded or destroyed, but large tracts of wet forest remain on the less accessible slopes and valleys. Trees were inventoried in

twenty-two 30 × 30 m square plots, which were randomly placed in undisturbed forests in the SWG; the total area sampled was 1.98 ha. Plots were located between latitudes 8°24′ and 9°50′ N.

The central Western Ghats (CWG) is a region where wet evergreen forest generally occurs at elevations of less than 1000 m in regions with high rainfall. Expanses of low-elevation dipterocarp forests are replaced at higher elevations by forests dominated by *Poeciloneuron indicum*. Trees were inventoried for 14 plots from the CWG distributed between latitudes 12°32′ N and 14°51′ N. The plots ranged from 0.14 to 0.16 ha in area and the total area sampled was 2.2 ha. Seven of these plots were located along a 35-km north-easterly rainfall gradient created in the Kogar region of Shimoga district in Karnataka by the south-west monsoon (Garrigues, 1999).

Elevation of the upper plateau of the Nilgiris averages 2000 m above sea level (a.s.l.), and montane forests, known locally as 'sholas', occur as patches in the hollow and sheltered valleys. Trees were inventoried for twenty-three 30 × 30 m plots randomly located within eight large sholas (> 0.9 ha) in the Korakundah–Upper Bhavani region in the south-west Nilgiris. The total area sampled was 2.07 ha. These sholas were located between latitudes 11°13′ and 11°14′ N at 2100–2300 m a.s.l. Data from a 0.2-ha plot located in Attapadi (Pascal, 1988) situated south of the Nilgiri plots (11° N), but at a lower elevation (900 m), were used for the large scale but not for the regional analyses.

Altitudinal and climatic diversity

We chose variation in elevation (m a.s.l.) as an indicator of topographic diversity and compared the ranges in elevation between the three regions. The elevation of each site was obtained from source publications for the CWG sites, and was directly measured with a pocket altimeter for the SWG and Nilgiri sholas. We calculated the coefficient of variation (CV) in elevation for the SWG and CWG but not for the Nilgiris, where the maximum difference in elevation was 200 m a.s.l.

We obtained accurate rainfall statistics for 47 sites either directly through meteorological stations operated in many parts of the WG by government agencies and private companies, or through source publications, which also used data from the same sources (Pascal, 1988). Rainfall data were obtained from rain gauges located fairly close (< 5 km) to the study plots. Using the available data, mean monthly and annual rainfall were computed for each site. Length of the dry season is defined as the number of consecutive months with monthly rainfall averaging < 100 mm. Data on monthly and annual rainfall were obtained for the years 1990 to 2002 for three CWG sites, and from source publications for the remaining sites (Pascal, 1988), and from rainfall gauges near the study plots for the Kogar sites (Garrigues, 1999). Monthly rainfall data for 13 years were available for six sites in the SWG, and for 6 years for three other sites. For each of the remaining 13 sites, which were all far from settlements, we estimated the average annual rainfall and dry season length using a bioclimatic map constructed from available meteorological data (Pascal, 1982). For further details on the climatic data for these two regions see Davidar *et al.* (2005). Monthly rainfall data from 1994

to 2003 for the Nilgiri sites were obtained from a Korakundah Tea Estate rainfall gauge within 5 km of all our study sholas, and the range in annual rainfall was taken for the 10-year period. We calculated the CV in annual rainfall and seasonality for the CWG and SWG where we had spatial data, but not for the Nilgiri plots, where the data were from just one rainfall gauge.

We evaluated relationships between the geographical co-ordinates of each site, elevation, annual rainfall and seasonality, applying correlation analyses to the whole dataset. The Nilgiris were represented by just one data point, and we used the median latitude, longitude and elevation and rainfall recorded at the closest rain gauge. We used subsets of the data to assess regional and local patterns within the CWG and SWG.

Species richness, diversity and turnover

We correlated species richness (*S*) and species diversity, as measured by Fisher's alpha (Fisher *et al.*, 1943), with latitude, longitude, annual rainfall and seasonality to see whether differences in diversity between sites influence turnover (Lennon, 2000; Lennon *et al.*, 2001). Fisher's alpha (α) is defined by the equation $S = \ln \alpha(1 + n/\alpha)$, where *S* is species richness and *n* is the number of individual trees on the plot.

In order to assess species similarity between sites, we calculated Sorensen's index of similarity (SI) as a measure of the proportion of species shared by two plots (Magurran, 1988; Colwell, 2005). Sorensen's index is $2j/(a + b)$, where *j* is the number of species common to both plots, *a* is the number of species in plot A and *b* is the number of species in plot B. SI ranges from 0 to 1, with 0 indicating no species in common and 1 indicating that the two sites have identical lists of species. We did not use the Mantel test because we wanted to make these results more comparable to a similar study by Condit *et al.* (2002) in Neotropical forests.

Nestedness is the circumstance whereby the set of tree species on a plot is a subset of the tree species on any more diverse plot. If plots along an environmental gradient show nestedness, then some factor is simply excluding species; it is not favouring new ones. We tested whether the species occurrence matrix was nested following Atmar & Patterson (1995). The program maximally packs the matrix, reordering rows and columns so as to concentrate presences in the upper left-hand corner of the matrix (Wright *et al.*, 1998). The packed matrix is then compared with randomly generated matrices using Monte Carlo simulations. The relative distances of these presences and absences along the diagonal axis (see Atmar & Patterson, 1993, for further details) are used to generate a matrix temperature that provides a standardized measure of matrix disorder. A perfectly nested matrix has a temperature of 0° and a completely disordered matrix 100° (Atmar & Patterson, 1993; Wright *et al.*, 1998).

SI values were regressed against the natural logarithm of the distances (km) to measure beta diversity. As site pairs are dependent, since there is correlation between the vegetation on nearby plots, we analysed beta diversity by calculating confidence intervals for regression coefficients by bootstrapping. We estimated mean values and confidence intervals for 600 to 1000 randomly extracted site pairs using SYSTAT (SPSS Inc., 2000). We

used a sample size of 600 for data bases with fewer than 12 plots and 1000 for data bases with more than 12 plots.

We assessed beta diversity at the scale of the WG, and then at regional and local scales. The large-scale analysis used data from all 60 plots distributed from 8°24′ N to almost 15° N. In order to test whether differences in seasonality between sites were responsible for beta diversity along the latitudinal axis, we regressed SI with log distance, and with differences in seasonality (months) between sites. We controlled for the effect of elevation by selecting only low-elevation plots (< 800 m a.s.l.) and then we controlled for latitudinal effects by using only data from SWG plots. In order to test whether beta diversity in the Kogar region was due to the gradient in annual rainfall, we regressed SI against log distance and SI against the difference in annual rainfall between plots.

The regional scale analyses compared beta diversity between the SWG, CWG and the Nilgiris. The local scale analyses compared beta diversity for Nilgiri plots that were > 1 km but < 6 km apart, seven Kogar plots < 25 km apart (13°53′ N to 14°05′ N), and 11 SWG plots (8°27′ N to 8°36′ N) that were < 10 km apart in medium-elevation forests (> 800 but < 1500 m a.s.l.).

We compared beta diversity between upper strata and understorey species in each region. Upper strata species were defined as those from the canopy, subcanopy and emergent strata (> 15 m), whereas understorey species were trees < 15 m in height growing in the forest interior (for further details see Davidar *et al.*, 2005). However, for the short-statured trees in the Nilgiri plots, we used 10 m as the limit between the upper strata and understorey, and excluded edge species. Data from plots separated by > 1 km were used for the analyses.

We compared beta diversity for the set of species dispersed by animals, and those dispersed by wind or gravity. Dispersal modes were evaluated based on literature descriptions (Gamble & Fischer 1915–1932; Saldanha & Nicholson, 1976; Matthew, 1981, 1982, 1999; Saldanha, 1984; Ganesh & Davidar, 2001).

We tested for differences in rates of species turnover in different regions, life-forms and dispersal modes by comparing the slopes of the regression equations using *t*-tests. Residuals and *P* values were obtained from outputs of regression analyses using just half of each data set, randomly extracted from the data base. The critical value of the *t*-tests was the sum of the two residual degrees of freedom, namely $\upsilon = (n_1 - 2) + (n_2 - 2)$. The computations were done by hand.

RESULTS

We recorded a total of 353 tree species in our plots. The species richness was higher in the SWG plots (264) than the CWG (159) and the Nilgiri plots (58). The SWG and CWG shared 97 of the 353 (27%) species and the Nilgiris and SWG shared 17 (5%) species.

Climatic patterns

The ranges and CV for elevation, seasonality and mean annual rainfall were higher in the SWG than the CWG (Table 1). Over

Table 1 Ranges and coefficient of variation in elevation (m), mean annual rainfall (mm) and seasonality (months) in the three regions

Variables	Statistics	SWG (*n* = 22)	CWG (*n* = 14)
Elevation (m)	Minimum	250	200
	Maximum	1550	900
	CV	0.332	0.310
Mean annual rainfall (mm)	Minimum	2000	2000
	Maximum	5900	5800
	CV	0.297	0.228
Dry season (months)	Minimum	1	4.5
	Maximum	4.5	6.5
	CV	0.378	0.087

SWG, southern Western Ghats; CWG, central Western Ghats.

the WG, seasonality increased with increasing latitude ($r = 0.80$, $P < 0.0001$) and decreasing elevation ($r = -0.61$, $P < 0.0001$). There was no significant correlation between elevation, annual rainfall and seasonality for the CWG sites. However, for the SWG sites, seasonality decreased with increasing annual rainfall ($r = -0.71$, $P < 0.0001$) and with increasing elevation ($r = -0.70$, $P < 0.0001$). There was no significant correlation between elevation, annual rainfall and seasonality in Kogar or among 11 SWG plots between 800 and 1500 m a.s.l.

Patterns of turnover at different scales

Similarity declined significantly and steeply with distance between inventory plots along the WG, suggesting that the latitudinal gradient in length of the dry season enhances the rate of beta diversity (Table 2 & Fig. 2). Although we could not look at the effects of the seasonality gradient directly, beta diversity decreased significantly with differences in seasonality in the low-elevation sites and the SWG sites (Table 2 & Fig. 3). Distances between sites doubled the R^2 values for low-elevation sites but remained the same for SWG sites, indicating that seasonality differences are important independent of distance between plots (Table 2). The low R^2 values for the SWG sites indicate that distances and seasonality differences were both fairly small within the SWG.

Fisher's alpha was lower at higher latitudes ($y = 22.83 - 0.01x$, $n = 60$, $R^2 = 0.20$, $P < 0.001$). The number of species per plot, however, was not correlated with latitude ($y = 32.62 - 0.003x$, $n = 60$, $R^2 = 0.004$, n.s.) for the simple reason that the more northerly plots were larger. Therefore beta diversity was not driven by differences in species richness between plots (Lennon *et al.*, 2001).

Regional trends differed: the CWG had higher levels of species similarity and rates of species turnover compared with the topographically heterogeneous SWG, although the slopes did not differ significantly ($t = 0.12$, n.s.; Table 2 & Fig. 2). The Nilgiris had higher levels of species similarity than the CWG but species turnover between these two regions did not differ significantly
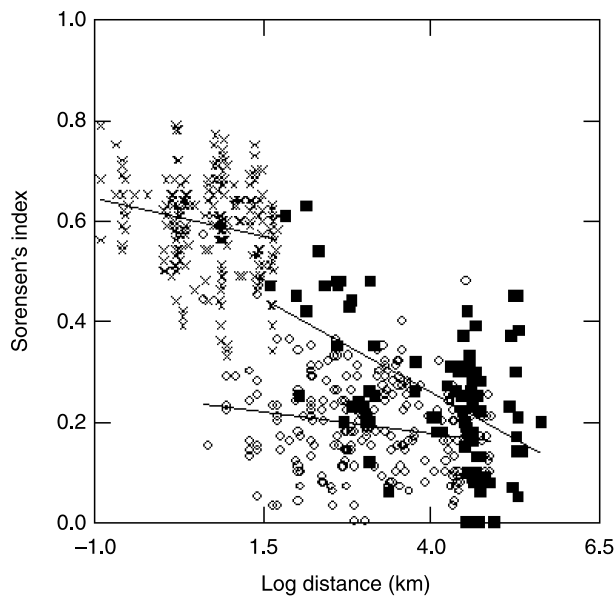
Figure 2 Relationship between Sorensen's index and log distance (km) in the southern Western Ghats (open circles), central Western Ghats (black squares) and the Nilgiris (crosses).

Figure 3 Relationship between Sorensen's index and seasonality differences between low-elevation (< 800 m a.s.l.) sites

($t = 0.167$, $P > 0.5$; Table 2 & Fig. 2). The rate of decline of species similarity with distance did not differ significantly between the SWG and the Nilgiris ($t = 0.007$, n.s.; Table 2 & Fig. 2).

Species richness among the CWG plots was not correlated with latitude ($r = -0.14$, n.s.), longitude ($r = -0.16$, n.s.) or annual rainfall ($r = -0.23$, n.s.), indicating that the results did not reflect differences between plots in species richness. The species distribution patterns in the CWG were not significantly nested as the matrix temperature of 42.82° did not differ significantly from that (52.29°) of randomly generated matrices.

Similarity in species composition declined faster with distance in the Kogar region than in medium-elevation sites in the SWG, although the slopes did not differ significantly ($t = 0.79$, $P = 0.4$;
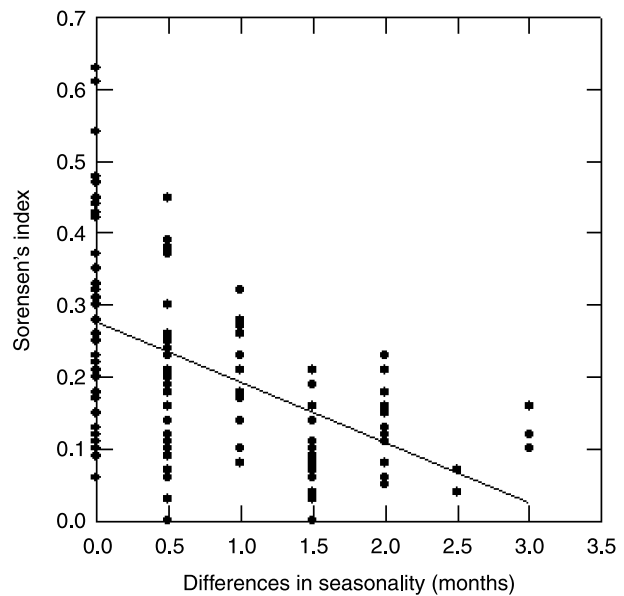
Table 2). In the Kogar region, mean rainfall decreased from 5037 to 4293 mm as one progressed further east from the ridge crest, while species richness increased from 33 to 46 per plot along the same gradient. Species richness declined significantly with increasing elevation ($r = -0.86$, $P = 0.01$) and increasing annual rainfall ($r = -0.93$, $P = 0.002$), and rainfall increased with increasing elevation ($r = 0.68$, $P = 0.09$), but not significantly so. Rainfall varied considerably between sites in the Kogar region, but not the length of the dry season. The differences in rainfall between plots did not influence beta diversity (Table 2).

The pattern of species distribution in the Kogar region was not significantly nested since the matrix showed greater disorder than expected by chance [the matrix temperature of 66.25° was

Table 2 Relationship between Sorensen's index (SI), log distance (km) and seasonality differences (months) using bootstrap estimation

Region	Intercept (SI) (95% CI)	Slope (95% CI)	R^2	n	P
All sites	0.558 (0.555 to 0.561)	−0.086 (log distance) (−0.086 to −0.085)	0.71	1728	<0.0001
All low-elevation sites (< 800 m a.s.l.)	0.511 (0.504 to 0.518)	−0.062 (log distance) (−0.063 to −0.061)	0.44	125	<0.0001
All low-elevation sites (< 800 m a.s.l.)	0.277 (0.274 to 0.280)	−0.087 (seasonal diff.) (−0.089 to −0.084)	0.27	125	<0.0001
CWG sites	0.551 (0.528 to 0.574)	−0.074 (log distance) (−0.080 to −0.069)	0.29	91	<0.0001
SWG sites	0.246 (0.235 to 0.248)	−0.017 (log distance) (−0.018 to −0.014)	0.04	231	0.004
SWG sites	0.217 (0.214 to 0.219)	−0.022 (seasonal diff.) (−0.024 to −0.020)	0.04	231	0.002
Nilgiris	0.604 (0.602 to 0.607)	−0.021 (log distance) (−0.023 to −0.018)	0.01	211	n.s.
CWG: Kogar sites	0.968 (0.957 to 0.979)	−0.221 (log distance) (−0.225 to −0.217)	0.49	21	<0.0001
CWG: Kogar sites	0.386 (0.382 to 0.390)	−0.000 (rainfall diff.) (0.000 to −0.000)	0.02	21	n.s.
SWG: elevation > 800 m	0.283 (0.272 to 0.294)	−0.026 (log distance) (−0.030 to −0.023)	0.08	66	0.02

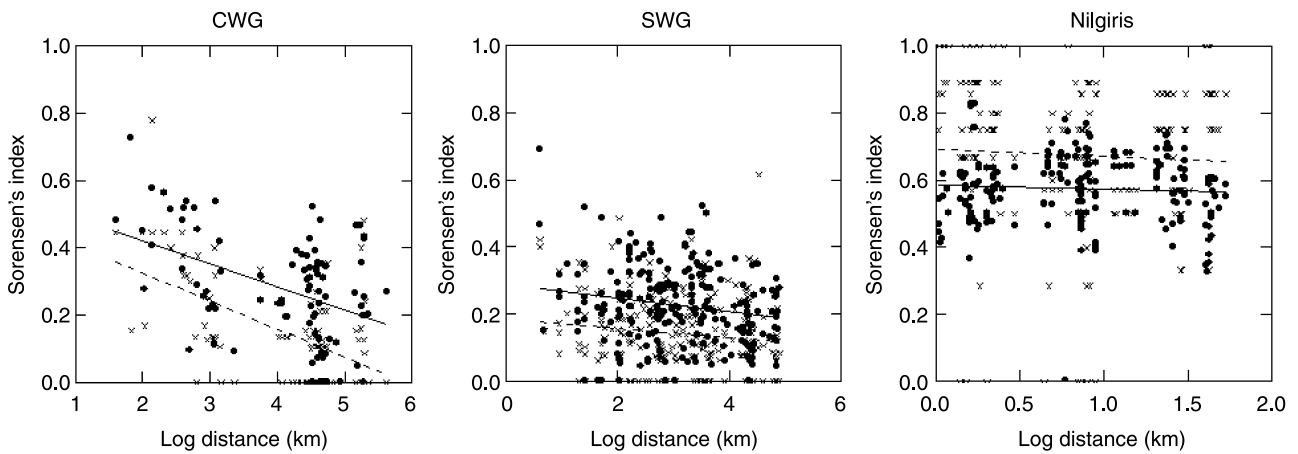CWG, central Western Ghats; SWG, southern Western Ghats.

Figure 4 Relationship between Sorensen's index and log distance (km) among trees of the upper strata (closed circles, solid line) and understorey (crosses): CWG, central Western Ghats; SWG, southern Western Ghats.

significantly higher than that of randomly generated matrices with a mean temperature of 52.29° (Atmar & Patterson, 1993)]. This suggests that the rapid beta diversity decrease with distance in this region was not due to nestedness along this gradient; disappearing species were at least partly replaced by new ones.

There were more species in the upper strata than the understorey (199 in the upper strata and 141 in the understorey). Of eight species common to all three regions, seven were from the upper strata and one from the understorey. About half the species of either stratum were recorded in only one region. A higher proportion of tree species belonged to the upper strata in the CWG and Nilgiris than in the SWG (Table 3). In the CWG and SWG, species similarity among trees of the upper strata was higher than that of the understorey, whereas this was the reverse in the Nilgiris, where species richness among understorey trees was low (Table 3 & Fig. 4).

There was no significant difference in beta diversity between the two strata for the three regions (Fig. 4 & Table 4). Beta diversity did not differ significantly between vertebrate-dispersed and mechanically-dispersed species in either the CWG ($t = 0.0097$, n.s.) or the SWG plots ($t = 0.0092$, n.s.). Most species (95%) in the Nilgiri plots were dispersed by vertebrates.

DISCUSSION

In the rain forests of the WG and the Nilgiri Hills, the similarity of tree species composition in different plots, as measured by the SI, decreases in linear proportion to the increase in the logarithm of the distance between the plots. In the WG, the length of the dry season increases from south to north due to the timing

Table 3 Species richness of trees in the upper strata and understorey. All three sites: $\chi^2 = 16.36$, d.f. = 2, $P = 0.0003$; CWG and Nilgiris: $\chi^2 = 7.48$, d.f. = 1, $P = 0.006$; CWG and SWG: $\chi^2 = 3.23$, d.f. = 1, n.s.; SWG and Nilgiris: $\chi^2 = 15.55$, d.f. = 1, $P = 0.0001$

Regions	Upper strata	Understorey	Total
CWG	100	58	158
SWG	134	113	250
Nilgiris	45	9	54

CWG, central Western Ghats; SWG, southern Western Ghats.

Table 4 Relationship between Sorensen's index and log distance (km) for trees of the upper strata and understorey

Region	Sorensen's index (95% CI)	Log distance (km) (95% CI)	R^2	n	P	t-test*
CWG upper strata	0.555 (0.544 to 0.566)	−0.069 (−0.071 to −0.066)	0.19	91	<0.0001	$t = 0.025$, n.s.
CWG understorey	0.475 (0.464 to 0.487)	−0.080 (−0.083 to −0.078)	0.29	91	<0.0001	
SWG upper strata	0.267 (0.259 to 0.275)	−0.018 (−0.020 to −0.016)	0.13	300	<0.0001	$t = 0.043$, n.s.
SWG understorey	0.217 (0.209 to 0.224)	−0.016 (−0.018 to −0.014)	0.09	300	<0.0001	
Nilgiri upper strata	0.583 (0.580 to 0.587)	−0.010 (−0.013 to −0.007)	0.003	211	n.s.	$t = 0.034$, n.s.
Nilgiri understorey	0.690 (0.682 to 0.698)	−0.021 (−0.028 to −0.014)	0.002	211	n.s.	

*Comparison between strata.

CWG, central Western Ghats; SWG, southern Western Ghats.

and direction of the monsoon winds (Pascal, 1988). The alpha diversity of trees increases with decreasing seasonality along the latitudinal gradient of the WG (Davidar et al., 2005). Therefore it is likely that high beta diversity along the latitudinal gradient is driven by seasonality as well.

O'Brien et al. (2000) have noted that, at the macroscale, variation in the length and quantity of rainfall is an important correlate of species richness. This is probably because water stress during the dry season is a constraint for plants. Wright (1992) observed that, in the tropics, tree diversity was lower not only where annual rainfall was lower, but especially where dry season was longer: he suggested that long dry seasons both reduced pest pressure, a factor that helps maintain tree diversity (Janzen, 1970; Connell, 1971; Leigh et al., 2004), and excluded drought-intolerant tree species. Condit et al. (1995) demonstrated that severe drought can be a major cause of mortality for tropical trees and shrubs, to which some species are far more sensitive than others: Engelbrecht & Kursar (2003) and Engelbrecht et al. (2005) showed experimentally that there is large interspecific variation in drought tolerance among tree seedlings. A dry season, therefore, could limit the distribution of many plants and thereby increase beta diversity because species whose seedlings are more likely to be killed by severe drought tend to be limited to regions with weaker dry seasons.

From the mountain crestline to a point 35 km eastward in the Kogar region of the CWG, annual rainfall decreases from 6449 to 2050 mm (Garrigues, 1999), driving a steep decline in tree diversity. We used a subset of the Kogar plots that receive an annual rainfall > 4000 mm, and show that, counter-intuitively, species richness decreases with an increase in annual rainfall, but this is because rainfall increases with elevation in the Kogar plots, and forests at higher elevations tend to be dominated by species-poor *Poeciloneuron indicum* stands. Beta diversity is high along this gradient and could be driven by the rainfall gradient, although the results are not conclusive. Species turnover was rapid along the steep rainfall gradient in central Panama from the wetter Caribbean to the drier Pacific shore (Condit et al., 2002). Along this same gradient, tree diversity on small plots declines rapidly from the wet ridges near the Caribbean to dry forest plots near the Pacific coast (Pyke et al., 2001). Therefore it is likely, at least for the WG, that gradient in annual rainfall is a more local phenomenon than gradient in seasonality.

Beta diversity rates were slower in the topographically heterogeneous SWG at both regional and local scales than in the CWG. This is contrary to what has been described for Neotropical forests, where a higher turnover in the Panamanian plots has been partly attributed to a greater variation in topography (Condit et al., 2002) and the distribution of Melastomataceae and ferns in western Amazonia was largely environmentally determined (Tuomisto et al., 2003). Even locally in the SWG, when only medium-elevation forests were considered, beta diversity was low.

A large species pool could also reduce the rate of species turnover. Species richness was much higher and species similarity lower on SWG than on CWG plots. Similarly, forests in western Amazonia had far more tree species per hectare, and far lower beta diversity, than did forests in central Panama (Condit et al., 2002).

Condit et al. (2002) have suggested that dispersal limitation might be more obvious in regions with less habitat variation, such as the Amazonian forests. Indeed the CWG, where conditions were more homogeneous, had higher levels of beta diversity. However, the rate of beta diversity was not higher in the upper Nilgiri plateau, which is more homogeneous with regard to rainfall and elevation than the CWG or the SWG.

Dispersal limitation could also alter the beta diversity rates between different life-forms (Nekola & White, 1999). The higher levels of similarity between the trees of the upper strata suggest either that understorey species are more dispersal limited or that large trees have wider ranges than shrubs. Trees in the British flora have larger range sizes than shrubs (Kelly, 1996), and widespread species in the Amazonian rain forests are often tall trees (Pitman et al., 2001). In this study, rates of beta diversity did not differ for trees in different forest strata, or trees with different dispersal modes, suggesting that beta diversity is independent of these tree characteristics.

The Nilgiri plots are anomalous in having few species, low turnover and high levels of similarity between sites. Kukkal shola, located in the Palni ranges about 150 km south of the Nilgiris, at an elevation of about 2000 m, shared > 50% of the Nilgiri species (D. Mohandass, pers. obs.), indicating the relative homogeneity of the montane forests in the Nilgiri and Palni Hill ranges. Loehle (1998) identified temperature as a key parameter determining the northern distributional limits of North American trees. Many species of trees are not resistant to frost (Latham & Ricklefs, 1993; Turner et al., 1996), and a glacial event could eliminate species in a mountain-bounded environment (Whittaker et al., 2001). It has been observed that recurrent frosts in the Nilgiris prevent the frost-intolerant shola trees from colonizing open sites (Meher-Homji, 1967).

In conclusion, our study shows that beta diversity among trees of the wet forests is driven primarily by climate. The latitudinal gradient in seasonality appears to drive beta diversity at the macroscale, and local gradients in rainfall could be influential locally. Topographical variation was not important. The role of dispersal limitation was not obvious, but similar rates of turnover between upper strata and understorey species, and vertebrate and non-animal dispersed species, suggest that dispersal limitation is not a serious contributor to species turnover here.

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