



Changes in rain forest tree diversity, dominance and rarity across a seasonality gradient in the Western Ghats, India

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ABSTRACT

Aim We assessed the effects of latitude, altitude and climate on the alpha diversity of rain forest trees in the Western Ghats (WG) of India. We tested whether stem densities, dominance, the prevalence of rarity, and the proportion of understorey trees are significantly correlated with alpha diversity.

Location The WG is a chain of mountains c. 1600 km in length, running parallel to the western coast of the Indian peninsula from above 8° N to almost 21° N latitude. Wet forests occur as a narrow strip in regions with heavy rainfall.

Methods To assess tree diversity we used data from 40 small plots, < 1 ha in area, where all trees ≥ 3.18 cm d.b.h. had been inventoried. These plots were distributed across 7 latitudinal degrees and at elevations between 200 and 1550 m. Fisher's alpha was used as a measure of diversity. For each plot, the proportion of trees belonging to the understorey, the proportion of trees belonging to the most abundant species in the plot, as a measure of dominance, and the proportionate representation of singletons, as a measure of rarity, were estimated, and correlated with Fisher's alpha, elevation, rainfall and seasonality.

Results Annual rainfall and seasonality increased towards the north, but were not significantly correlated. Tree diversity increased significantly with decreasing seasonality. Tree diversity was not significantly correlated with stem density or with the proportion of understorey tree species, but was significantly correlated with tree dominance and rarity. Dominance increased and rarity significantly decreased with increasing seasonality.

Main conclusions This study demonstrates that seasonality influences rain forest tree diversity in the WG of India. The relationship between alpha diversity, dominance and rarity lends correlative support for the Janzen–Connell pest pressure hypothesis.

Keywords

Alpha diversity, India, Janzen–Connell hypothesis, pest pressure, seasonality gradient, tropical rain forest, Western Ghats.

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INTRODUCTION

Rainfall and seasonality are important predictors of alpha diversity in tropical rain forests. Why this relationship exists, however, is not clearly understood (Phillips *et al.*, 1994; Clinebell *et al.*, 1995; Leigh, 1999; Pitman *et al.*, 2002; ter Steege *et al.*, 2003). Do wet aseasonal forests support more tree species because they have higher stem density (ter Steege *et al.*, 2003), because trees on wetter soils are shorter-lived (Phillips

et al., 1994), because understorey plants live longer where there is no drought (Huston, 1994; Pitman *et al.*, 2002), because light gaps are more frequent (Phillips *et al.*, 1994) or because a greater abundance of species-specific pests and pathogens allow more species to coexist than in drier forests (Janzen, 1970; Connell, 1971; Givnish, 1999; Wright, 2002)? The Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971) suggests that tropical rain forests are diverse because species-specific pests cause mutual repulsion among conspecifics

(Janzen, 1970; Connell, 1971), largely by diminishing recruitment near conspecific adults (Wills & Condit, 1999; Peters, 2003).

The rain forests of the Western Ghats (WG) of India provide a good model system for testing the relative effects of rainfall and seasonality on tree diversity, because the monsoon regime causes dry season lengths to be longer where annual rainfall is higher (Pascal, 1988), contrary to the climatic pattern experienced by Neotropical forests. The independent gradients in rainfall and seasonality allow correlative tests of hypothesis relating to alpha diversity. In this study we ask how alpha diversity of trees in the rain forests of the WG is related to climatic variables such as annual rainfall and seasonality, by using data from tree inventories ranging across 7 latitudinal degrees. We then test four specific hypotheses: is a plot's tree diversity correlated with (1) the density of stems on the plot; (2) the proportion of species on the plot that are represented by understorey species, whose maximum height is less than 15 m; (3) the proportion of trees on the plot belonging to its most common species; or (4) the proportion of species on the plot that is 'rare'? We evaluate the association between the above variables and the climatic gradient prevalent in the WG.

Rain forests occur as a narrow strip along the WG from the southern tip of India to above 16° N latitude. These rain forests (or wet evergreen forests) have lower species richness (species ha⁻¹) than the extensive forests of the Amazon or Southeast Asia (Pascal & Pelissier, 1996; Parthasarathy & Karthikeyan, 1997). Because they have been well described floristically and many aspects of their biology are well known, they can be used to test several hypotheses on diversity that can be addressed by a correlative approach. Without long-term data on species biology, we cannot address processes in detail, but some simple observations may help us to discard certain hypotheses and allow future research to focus on processes that appear more likely to be important.

STUDY AREA

The WG, a global biodiversity hotspot (Myers, 1990), is a chain of mountains *c.* 1600 km in length, running parallel to the western coast of the Indian peninsula from above 8° N to almost 21° N latitude (Fig. 1).

The rain forests of the WG have been influenced considerably by continental movements and associated climate changes. As India drifted northwards in the Paleocene, its flora was enriched by colonization from Africa (Morley, 2000). The rain forest has undergone large-scale contraction due to increasing aridity over the subcontinent and now exists as a narrow belt along the WG. It recolonizes the grasslands when human disturbance is low (Puyravaud *et al.*, 1994, 2003). The flora is characterized by many relictual species and a high proportion of species endemic to the WG (Ramesh *et al.*, 1997).

Many inventories have been conducted to describe the floristics and assess stem densities, species diversity and basal area of relatively pristine forests (Pascal, 1988; Pascal &

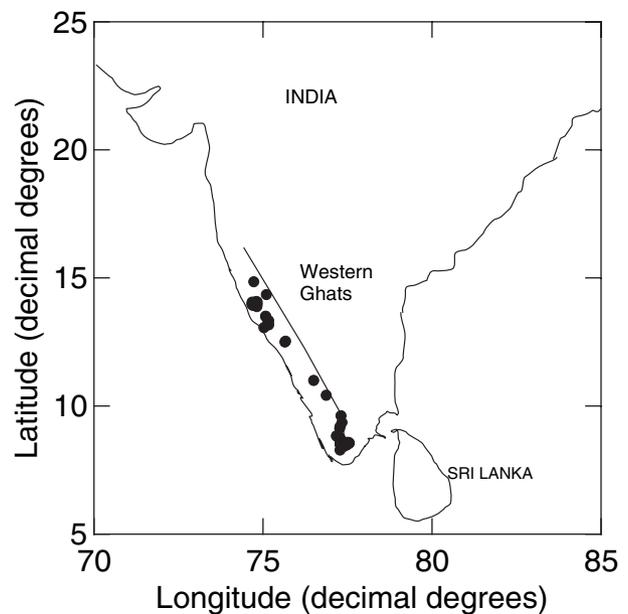


Figure 1 Map of the study area with location of the plots (solid circles).

Pelissier, 1996; Parthasarathy & Karthikeyan, 1997; Ayyappan & Parthasarathy, 1999; Parthasarathy, 1999, 2001). A typology of the forests has been conducted using bioclimatic information (Pascal, 1988), but this is the first large-scale analysis of alpha diversity for rain forest trees in the WG.

The length of the major dry season, which falls between the South West and the North East monsoons, is widely supposed to be the most important influence on floristic types in the Ghats (Pascal, 1988). The length of the dry season increases from the south to the north, because the South West monsoon lasts longer towards the south. The North East monsoon only affects the southern region, where it further decreases the length of dry seasons there. In addition, orographic effects create sharp west–east gradients in rainfall (Ramachandran & Banerjee, 1983; Gunnell, 1997).

MATERIALS AND METHODS

Plot characteristics

Tree inventories from 40 small plots, located at sites from *c.* 8°24' to 14°51' N latitude, were used to assess patterns of tree diversity (full details can be found in Appendix S1 in the Supplementary Material). These plots were chosen from a data base of 135 plots, as follows. To be chosen, a plot must have 75 or more stems, and its site must have over 2000 mm of rain per year and high basal area for that climatic zone (characteristic of historically unlogged forests: Elouard *et al.*, 1997), and it must have suffered low human disturbance (no record of logging, as judged from Forest Department working plans and low current human impact). Total area sampled was 4.65 ha. These plots, although laid by different investigators,

followed the same methodology. All stems > 3.18 cm diameter at breast height (d.b.h.) were identified and recorded. Species identifications in all plots were by experienced botanists and unidentified species indicated as such.

Plot sizes ranged from 0.09 to 0.2 ha. All stems \geq 3.18 cm (10 cm girth at breast height) were inventoried, and height recorded. Eight of the plots were from published sources and 32 from unpublished data (full details can be found in Appendix S1). Twenty-six of the plots were south, and 14 north of the Palghat Gap, a major break in the WG at around 10°50' N. Twenty-five plots, 30 × 30 m in dimension (0.09 ha), were laid in randomly selected sites (using geographical coordinates) in the southern WG (SWG), for the purpose of biodiversity characterization (Davidar *et al.*, unpubl. data). Seven 0.16-ha plots from the Kogar region were originally used as controls for assessing the effect of human disturbance on plant diversity (Garrigues, 1999; Puyravaud & Garrigues, 2002). The rest of the plots were from a published data base (Pascal, 1988), the number of individuals per species was estimated from information given in the publication. The geographical coordinates of the plots were transformed into the equivalent degree decimal units for analyses.

We used Fisher's alpha (Fisher *et al.*, 1943), which is relatively independent of plot size (Condit *et al.*, 1996; Leigh, 1999) to measure alpha diversity. The distribution of trees over species in 1-ha plots appears to follow a log series distribution (Leigh, 1999). In the forests studied by Condit *et al.* (1996), for any given number of contiguous stems, the number of species is roughly the same regardless of the lower diameter limit of stems sampled. Therefore, Fisher's alpha allows a relatively unbiased comparison of diversity on plots where different sizes and numbers of stems are sampled (Leigh, 1999).

Climatic parameters

Rainfall data were available between the years 1990 and 2002 for many sites. For 28 plots, the mean annual rainfall and dry season length were obtained for periods from 1 to 13 years, from meteorological stations located close to the site. Some of these plots were clustered within 5 km and shared a station.

For CWG plots there were monthly rainfall data for 1 year for eight sites, and 7–10 year data for another six sites. In the SWG there was monthly rainfall data for 13 years at six sites, and for 6 years at three sites in the Agastyamalai and Mahendragiri ranges. For 12 sites, which were far away from settlements, the average annual rainfall and dry season length for each site was obtained from bioclimatic maps (Pascal, 1982), and cross-checked with the location of the plots in topographic sheets to assess the intensity of the monsoon winds. For example, plots on the crest or the west-facing slope of a mountain might have a different rainfall profile from plots on the eastern slopes. Rainfall and seasonality from reference sites were used for sites with similar topographic profiles within a region. The subset of the plots with accurate climatic information was used for preliminary analyses, and as these

results did not differ from that of the full data set, all the plots were used for the analyses.

For sites where climatic data were available, the mean length of the dry season was estimated as the number of consecutive months where the monthly rainfall is < 100 mm. This was a biologically meaningful assessment of seasonality as it is related to the water holding capacity of the soil. In the Kodagu region (c. 12°30' N), where the soil is fairly deep, the available water capacity (AWC) was estimated as 81 mm m⁻¹ of soil (Peterschmitt, 1993), which is sufficient to avoid physiological drought in regions with long dry seasons and sufficient soil depth (Elouard *et al.*, 1997). Mean seasonality was calculated as the average length of the dry season for the given number of years. In sites with two monsoons and a major and minor dry season, the length of the longer dry season was used. The relationship between mean annual rainfall and mean seasonality were analysed for selected CWG and SWG sites for which > 6-year data were available.

The elevation for the unpublished inventory plots was measured using a pocket altimeter, and crosschecked with topographic maps.

Floristics

Species in the unpublished plots were identified through voucher specimens collected from each tree and deposited at the herbaria of the Salim Ali School of Ecology and Environmental Sciences, Pondicherry University and the French Institute of Pondicherry. Specimens were identified to species with the help of floras using vegetative and reproductive characters (Gamble & Fischer, 1915–1936; Saldanha & Nicholson, 1976; Saldanha, 1984; Pascal & Ramesh, 1987; Matthew, 1999). We also used herbaria of the French Institute of Pondicherry, Botanical Survey of India, Coimbatore and St Xavier's College in Palayamkottai. Few species remained unidentified.

Species–abundance relationships and stem density

To look at the species–abundance patterns, the density (stems ha⁻¹) was calculated for each species in each plot and averaged for all the plots. The densities were then log transformed and fitted to a normal curve. Normality was tested using the Kolmogorov–Smirnov (K–S) test.

Log stem densities were correlated with altitude, annual rainfall, mean seasonality and Fisher's alpha. Variables with significant correlations were used in multiple regression analyses.

Alpha diversity, altitude and climate

South of 9° N latitude, the transitional limit between low and medium elevation forests is near 800 m. As most of the medium elevation plots but two fell south of 9° N, we considered this altitudinal limit as suitable for our data set.

The effects of latitude on mean annual rainfall and mean seasonality, and the relationship between climatic variables and Fisher's alpha were analysed using correlations and linear regressions. Except for latitude and longitude, the data followed a normal distribution allowing for regression analyses. Separate analyses were conducted for the central WG (CWG) plots which lie north of 11° N, and the SWG plots, south of 11° N.

Effect of understorey species

Using the maximum heights of each species (Davidar, unpubl. data; Puyravaud, unpubl. data) and the forest stratum to which they belonged within the forest (Pascal, 1988), the species were assigned to the canopy (25–35 m), the subcanopy (15–25 m), the understorey (5–15 m) and the emergent layer (> 35 m). The proportion of species in each plot that belonged to the forest understorey was estimated and correlated with Fisher's alpha and climatic variables.

Dominance and rarity

The proportion of stems on a plot belonging to its most abundant species was used as an index of dominance. This was regressed against Fisher's alpha and mean seasonality.

We derived an index of rarity by totalling the number of species in a plot represented by just one individual, and taking the proportionate representation of these species among the plot's stems. Another index of rarity was derived by arranging trees in increasing order of abundance, counting the number of species required to account for one-tenth of the plot's stems, and dividing this by the total number of tree species on the plot. Both indices were used for the analyses and the one that gave a better fit was selected.

Statistical analyses

Correlations were performed between all the variables. Regression analyses were conducted between selected variables with significant correlations and sometimes non-significant correlations. All tests were conducted using Systat (version 10; SPSS Inc., 2000).

RESULTS

Patterns of rainfall and seasonality

Annual rainfall and seasonality increased significantly from south to north (Fig. 2), but were not significantly correlated with each other (Fig. 2, Tables 1 & 2). However, regional patterns differed and rainfall and seasonality were significantly correlated for the SWG sites, but not for the CWG sites (Fig. 3). The SWG sites had a greater variation in seasonality (range of CVs: 0.156–0.565) than the CWG sites (range of CVs: 0.078–0.216). These results suggest that inter-year variation in climatic parameters between sites is a result of the varying effect of the monsoon regime over the Ghats.

Stem densities, species richness and alpha diversity

The log density of species differed significantly from a normal distribution (K-S, $d = 0.11$, $P < 0.01$). Log stem density (stems ha^{-1}) was marginally related to latitude and rainfall but did not influence any other variable including Fisher's alpha (Tables 1 & 2).

Fisher's alpha values ranged from 2.72 in Bhagvati in the CWG to 28.7 in Vanamutti in the SWG. The mean value for Fisher's alpha for all 40 plots was 12.92 ± 0.87 (SE).

Fisher's alpha was not significantly correlated with either annual rainfall or altitude, but decreased significantly with increased seasonality in all plots (Tables 1 & 2). Fisher's alpha was lower for the medium elevation plots than for low elevation plots (Table 2; Fig. 4). When analysing regional trends, Fisher's alpha was not related to annual rainfall either in the CWG or the SWG (CWG: $n = 14$, $y = 13.63 - 0.001x$, $R^2 = 0.03$, n.s.; SWG: $n = 26$, $y = 9.86 + 0.001x$, $R^2 = 0.05$, n.s.), and was significantly related to seasonality for the SWG sites ($y = 21.23 - 2.36x$, $n = 26$, $R^2 = 0.20$, $P = 0.03$), but not for the CWG sites ($n = 14$, $y = 25.8 - 2.9x$, $R^2 = 0.12$, n.s.). This is probably because seasonality does not vary much between the CWG sites.

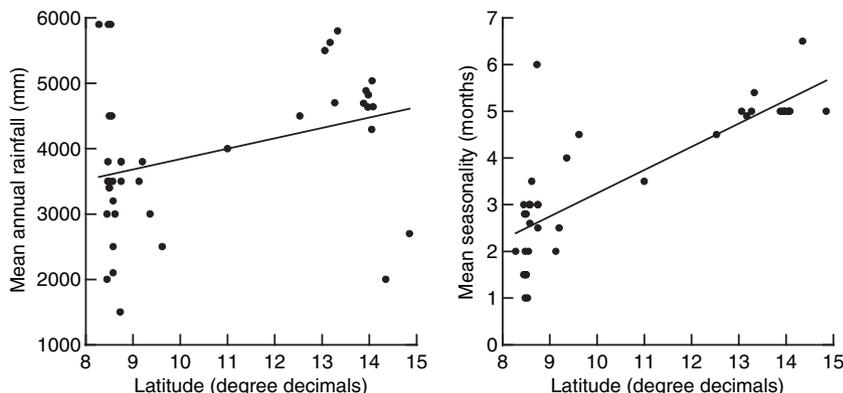


Figure 2 Latitudinal trends in annual rainfall and seasonality in the Western Ghats.

Table 1 Correlation coefficients of variables used in the study for 40 plots

| | Latitude (decimal degrees) | Altitude (m) | Rainfall (mm) | Seasonality | Log <i>N</i> | Fisher's alpha | Understorey species | Dominance |
|---------------------|-------------------------------|-----------------|------------------|-------------|--------------|-------------------|------------------------|-----------|
| Latitude | 1.00 | | | | | | | |
| Altitude | -0.66*** | 1.000 | | | | | | |
| Rainfall | 0.34 | 0.05 | 1.000 | | | | | |
| Seasonality | 0.82*** | -0.77*** | -0.04 | 1.00 | | | | |
| Log <i>N</i> | 0.52* | -0.33 | 0.45** | 0.36 | 1.00 | | | |
| Fisher's alpha | -0.31 | 0.22 | 0.00 | -0.46** | -0.06 | 1.00 | | |
| Understorey species | -0.32 | 0.23 | -0.06 | -0.15 | -0.05 | -0.1 | 1.00 | |
| Dominance | 0.14 | -0.22 | -0.11 | 0.41* | -0.02 | -0.78*** | 0.16 | 1.00 |
| Rarity | -0.68*** | 0.51* | -0.21 | -0.68*** | -0.24 | 0.69*** | 0.24 | -0.45** |

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

Table 2 Linear regressions between selected dependent and independent variables

| Dependent variable | Independent variable/s | Equation | <i>N</i> | R^2 | <i>P</i> |
|---------------------------|----------------------------|----------------------|----------|-------|----------|
| Mean annual rainfall (mm) | Latitude (decimal degrees) | $y = 1568 + 2.4x$ | 50 | 0.19 | 0.001 |
| Mean seasonality (months) | Latitude (decimal degrees) | $y = 2.24 - 0.005x$ | 50 | 0.77 | 0.0001 |
| Log stem density | Annual rainfall | $y = 4.33 - 0.0001x$ | 40 | 0.10 | 0.05 |
| Fisher's alpha | Mean seasonality | $y = 18.82 - 1.68x$ | 40 | 0.21 | 0.003 |
| Fisher's alpha | Dominance index | $y = 28.53 - 31.78x$ | 40 | 0.61 | < 0.0001 |
| Fisher's alpha | Rarity index | $y = 5.98 + 80.61x$ | 40 | 0.48 | < 0.0001 |
| Dominance index | Mean seasonality | $y = 0.38 + 0.04x$ | 40 | 0.17 | < 0.01 |
| Rarity index | Mean seasonality | $y = 0.16 - 0.02x$ | 40 | 0.45 | < 0.0001 |

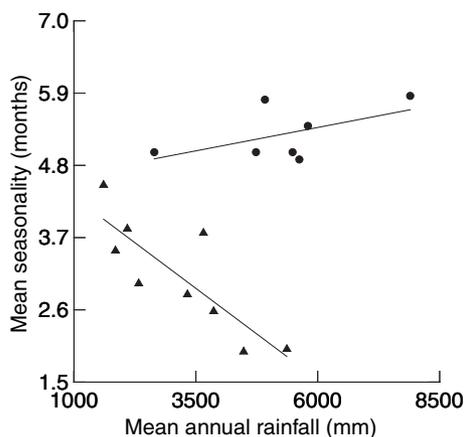


Figure 3 Relationship between annual rainfall and seasonality in seven CWG sites (circle) and nine SWG sites (triangle). CWG: $y = 4.52 + 0.0001x$, $n = 7$, $R^2 = 0.3$, n.s.; SWG: $y = 4.87 - 0.001x$, $n = 9$, $R^2 = 0.69$, $P = 0.006$.

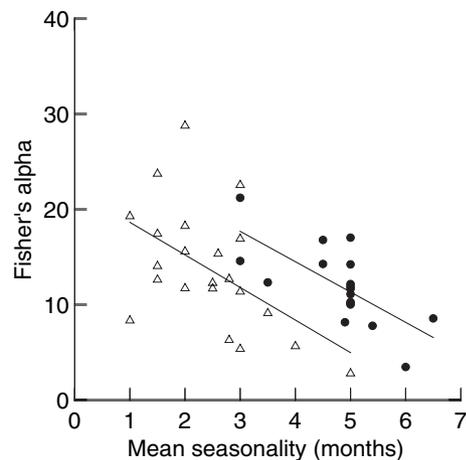


Figure 4 The relationship between seasonality and Fisher's alpha in low (circle) and medium (triangle) elevation plots. Altitude < 800 m: $y = 6.64 - 0.15x$, $n = 18$, $R^2 = 0.49$, $P < 0.001$; altitude > 800 m: $y = 3.53 - 0.08x$, $n = 22$, $R^2 = 0.27$, $P = 0.01$.

Dominance, the prevalence of rarity, and the proportion of species belonging to the understorey

We measured rarity by the proportion of stems in a plot contributed by species with only one tree apiece, because it provided stronger correlations than the alternative metric. The alternative measure seemed arbitrary where the species with one tree apiece accounted for more than 10% of the trees on the plot. Fisher's alpha decreased significantly with increasing

tree dominance in plots (Tables 1 & 2; Fig. 5), and increased significantly with the prevalence of rarity (Tables 1 & 2; Fig. 5). Dominance and rarity were significantly negatively correlated (Table 1). Dominance increased significantly with increasing seasonality (Tables 1 & 2; Fig. 5), whereas rarity declined significantly with increasing seasonality (Tables 1 & 2; Fig. 5).

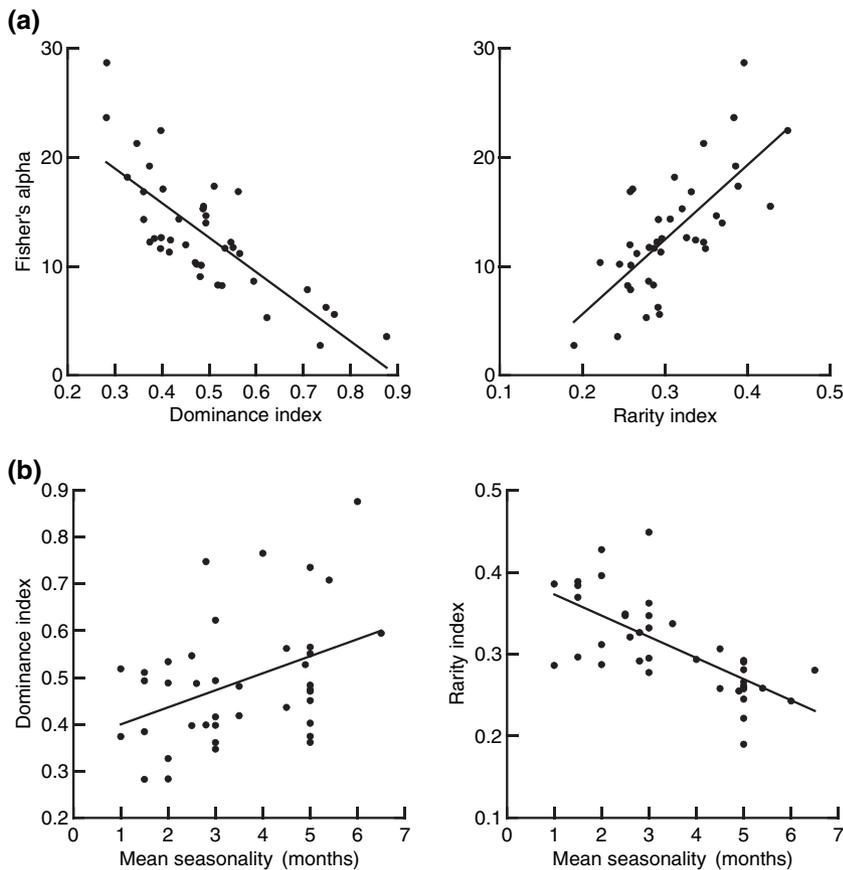


Figure 5 (a) The relationship between alpha diversity, tree dominance and rarity, (b) the relationship between dominance, rarity and mean seasonality.

Of the 32 species that dominated in the 40 plots, 21 (65%) were distributed across the seasonality gradient from regions with short, to regions with long dry seasons, and the rest were confined to sites with either short or long dry seasons.

DISCUSSION

The WG provides an arena for independently testing the effects of rainfall and seasonality on tree alpha diversity. This is because rainfall and seasonality are not correlated over the WG. The South West monsoon strikes the southern part of the WG first, and then advances northwards. It then retreats in reverse, creating a longer rainy period and shorter dry season length towards the south. Rainfall and seasonality were tightly correlated for sites in the SWG, whereas they were not in the CWG.

Our study indicates that seasonality, and not annual rainfall, is the variable that drives tropical rain forest tree diversity. Alpha diversity is related to seasonality both for the WG as a whole and within the SWG where there is a greater variation in dry season lengths. In Neotropical rain forests, species richness and diversity are related to annual rainfall and seasonality, as both are negatively correlated (Gentry, 1988; Clinebell *et al.*, 1995; Leigh, 1999; ter Steege *et al.*, 2003).

Alpha diversity for the WG sites decreased with altitude independently of dry season lengths. Species richness decreases with altitude for reasons that are not clearly understood

(Gentry, 1988; Lieberman *et al.*, 1996; Leigh, 1999). In Neotropical sites there was an initial increase of diversity with altitude probably due to the decrease in dry season lengths, but diversity declined at higher altitudes (Leigh, 1999). In our study Fisher's alpha was not significantly correlated with altitude, but diversity was lower for medium elevation sites than for the low elevation sites.

Do stem densities influence alpha diversity?

In the Amazon basin, Fisher's alpha tends to be higher where density of trees ≥ 10 cm d.b.h. is higher, perhaps because tree density is higher at wetter and less seasonal sites (ter Steege *et al.*, 2003), whereas in the WG, stem densities do not influence the alpha diversity of trees. Stem densities of trees in the WG tend to increase significantly with rainfall, as in the Neotropics (Wright, 1992), but were not related to seasonality.

Effect of understorey species

Higher alpha diversity in aseasonal forests has been attributed to an increase in the number of smaller tree species (Givnish, 1999; Pitman *et al.*, 2002; ter Steege *et al.*, 2003) and functional guilds in the understorey (Huston, 1994). In the WG, the proportion of species confined to the understorey does not influence alpha diversity.

Dominance, rarity and alpha diversity

Pitman *et al.* (2002) have suggested that higher species richness at Yasuni than at Manu in the Amazon basin could be due to the relative increase in the proportion of rare species. There were more species represented by one, two or three individuals at Yasuni than at Manu. In this study we find that Fisher's alpha increased significantly with rarity, and decreased significantly with dominance. Here, both rarity and dominance influence Fisher's alpha, as one would expect. Higher pest pressure in less seasonal sites would increase diversity by reducing the abundance of common species. If pest pressure is more intense in less seasonal forests, then rarity should decrease and dominance should increase with seasonality. These predictions are supported by our results. In aseasonal forests, insect activity is fairly even through the year (Wolda, 1983, 1988; Wright, 1992), and herbivores consume young leaves more rapidly than in drier forests (Coley & Barone, 1996). Higher pest pressure in aseasonal sites might maintain tree species at low densities whereas in more seasonal sites the common species will constitute a higher proportion of stems (Janzen, 1970). If relative abundance is governed primarily by pest pressure, then the most common species, which are the most successful at escaping pests, should occupy the widest range of habitats. However, if dominant species were restricted to long or short dry seasons, then the pest pressure hypothesis will not be supported. The majority (65%) of the 32 dominant species documented in these plots were distributed across the seasonality gradient.

Many studies have demonstrated the importance of density-dependent mortality in influencing tree distribution patterns in tropical rain forests (Condit *et al.*, 1992; Okuda *et al.*, 1997; Wills & Condit, 1999; Harms *et al.*, 2000; Peters, 2003), and seeds and seedlings do suffer higher mortality under the parent tree as predicted by the Janzen–Connell model (Augsburger, 1983, 1984; Howe *et al.*, 1985; Sinha, 1990; Wong *et al.*, 1990; Gilbert *et al.*, 1994). Givnish (1999) had suggested that density-dependent mortality should increase at wetter sites. Our study shows that dominance, the ability of one species to occupy a plot, and the increase of rare species at more aseasonal sites, are consistent with the predictions of the pest pressure hypothesis, but these results need to be tested more explicitly across seasonality gradients. Hille Ris Lambers *et al.* (2002) have shown that the proportion of tree species experiencing density-dependent mortality is similar in temperate and tropical forests although the intensity might differ. Similarly the intensity of pest pressure could vary across the seasonality gradient.

In conclusion, this study has demonstrated that seasonality is an important predictor of tree alpha diversity in the WG of India. It is likely that higher species diversity in the more aseasonal wet forests is due to pest pressure that maintains competitively superior tree species at lower densities. Our study suggests that similar processes could regulate alpha diversity in large, species-rich forests as well as in smaller, species-poor rain forests such as those in the WG.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1165/JBI1165sm.htm>

Appendix S1 Location and other information pertaining to 40 inventory plots used for the analyses.

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