Mesoscale Patterns in the Floristic Composition of Forests in the Central Western Ghats of Karnataka, India

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ABSTRACT

We describe the mesoscale floristic patterns in the central Western Ghats of Karnataka, India, through combined analysis of woody species abundance and stand structure data from a network of ninety-six 1-ha sampling plots spread across 22,000 km². A total of 61,906 individuals (≥10 cm gbh) comprising 400 plant species from 254 genera and 75 families were recorded. Euphorbiaceae, Rubiaceae, Lauraceae and Moraceae families constituted 23.5 percent of the total number of species encountered. The relative dominance of species was skewed with Poecilonueron indicum, Xyli a xylocarpa, Terminalia tomentosa and Anogeissus latifolia being dominant in some plots. Correspondence analysis (CA) and a nonmetric multidimensional scaling (NMDS) of plots by species abundances data showed similar arching patterns, with significant correlation between the first axis of CA and NMDS (r = 0.77). Hierarchical clustering of plot scores along the three first CA axes resulted in splitting the plots into five different categories that broadly reflect the major bioclimatic features of the region. A multiscale bootstrapping test indicated that categorization of the wettest (wet evergreen group 1 and 2) and driest (dry deciduous) groups were robust (P < 0.05 with 1000 bootstraps), while the remaining two transitional groups were uncertain (P = 0.12 and 0.26 for moist deciduous and semi-evergreen group, respectively). Principal component analysis revealed that plots with similar floristic composition can encompass contrastingly different physiognomic structures (canopy cover, canopy height and mean tree diameter) probably in relation to their levels of disturbance. Observed patterns in the floristic composition have been discussed in the light of the complex interaction between the bioclimatic and disturbance regimes that characterize the region.

Key words: bioclimatic influences; disturbance history; forest stand structure; indirect gradient analysis; regional patterns; tree species diversity.
close as possible to an equilibrium with the environmental conditions, at least at a human time scale (Pascal 1988; Davidar et al. 2005, 2007). The only available study based on a large network of plots (with a fixed number of 100 individuals per plot, thus sampling areas of 0.27–1.65 ha) spread across large spatial scales of the WG and covering various levels of disturbance regimes is that of Utkarsh et al. (1998). Consequently, mesoscale variations in species abundances in the forests of this region remain poorly understood and much is still to be learned from additional networks of forest plots.

Our paper makes one of the first such attempts based on an important network of ninety-six 1-ha sampling plots spread over ca 22,000 km² in the central WG of Karnataka, India. The main vegetation patterns are examined and described based on combined analysis of species abundance and forest stand structure data, and then discussed in the light of the complex interaction between the bioclimatic and disturbance regimes that characterize the region.

**METHODS**

**STUDY AREA.**—The study area (13°30′–15°15′ N, 74°15′–75°40′ E) falls within the administrative boundaries of Uttara Kannada, Shimoga and Chikmagalur districts of the State of Karnataka in south-western India (Fig. 1). The total area covered is 21,970 km² of the central WG region. It extends from the coastal plain of the Arabian Sea to the humid hill zone (locally called Malnad) across the WG ‘great escarpment’, and to the Karnataka plateau (Maidan), that recedes toward the eastern upland region.

The WG relief barrier orographically exacerbates the summer monsoon rains and is also responsible for a steep environmental cline from the plateau edge into the interior upland (Pascal 1982, Gunnell 1997). The windward side of the WG receives heavy rains with annual amount > 2000 mm, and commonly > 5000 mm near the crest of the Ghats. This diminishes toward the interior

![FIGURE 1. Location of sampling plots in the central Western Ghats region of Karnataka, India. The isolines indicate mean annual rainfall in mm (solid) and mean number of dry mo (sensu Pascal 1982; dotted). See text for details on the plot groups.](image)
regions, ranging from 2000 to 900 mm (Fig. 1). Between the coastline and the crest of the Ghats, at elevations < 800 m, mean coldest month temperature is around 23 °C, while in the hilly terrains at medium elevations (800-1400 m asl) it varies between 16 °C and 23 °C. Correlating with the sharp decrease in rainfall beyond the crest of the Ghats, the length of the dry season rapidly increases in the west–east direction. The dry season length increases from 4 to almost 7 mo from south to north of the study region, where a month being considered as dry (Pascal 1982) when rainfall (mm) is lower than twice the mean temperature (°C). From these bioclimatic characteristics, Pascal (1988) defined three main domains of potential forest vegetation in the WG region: wet evergreen > 2000 mm/yr, moist deciduous (MD) 1500-2000 mm/yr and dry deciduous (DD) < 1500 mm/yr. Soils of the study area are ferrallitic (laterites) to ferrosualic (red soils), with a massive development of kaolinite as a product of rock weathering where the annual soil water balance is consistently positive (i.e., > 1200 mm rainfall; Bourgeon 1989, Gunnell & Bourgeon 1997).

**Sampling Scheme and Data.**—Floristic data were collected from a network of ninety-six 1-ha biodiversity sampling plots (BSP) established by the Karnataka Forest Department (KFD) in 1996–1997 (Ramesh et al. 2009b). The original project aimed at delineating zones for management considerations based on forest status and distribution, along with details on anthropogenic pressures. Hence, covering large areas across various environmental (e.g., bioclimate) and disturbance (e.g., land use, human population density) gradients were prioritized over systematic sampling. In the 1-ha plots, all live individual trees and lianas that were equal and > 10 cm girth at breast height (gbh) were measured and tagged with serial numbers. The botanical identifications were supervised and checked by two of us (BRR and SVP) and conform to the reference taxonomy of the Herbarium of the French Institute of Pondicherry (HIFP). The species were later phenologically classified as evergreen or deciduous based on existing literature (Pascal 1986) and botanists’ expertise. Also, at the plot level, canopy height (m) and canopy cover (%) were estimated visually. Rainfall data for the plots were derived by interpolation of recorded rainfall for 336 stations followed over at least 10 yr since 1940, obtained from the Indian Meteorological Department and Directorate of Economics and Statistics, Government of Karnataka. Mean annual rainfall values at plot locations were estimated through ordinary kriging method available within the spatial analyst extension in ArcView GIS 3.1 (ESRI Inc., Redlands, CA). Data on dry season length are extrapolated from Pascal’s (1982) bioclimatic map.

**Statistical Analyses.**—We analyzed the patterns of species diversity by summarizing floristic data from the plots in a site-by-species abundance matrix. To discern patterns in the species distribution and plot composition, we performed a correspondence analysis (CA) on this matrix. The CA emphasizes poor plots and scarce species, an essential treatment for revealing the subtle floristic gradients (see Couteron et al. 2003). To ascertain that the patterns observed in the CA were not an artifact of the method, we compared the CA plots scores with that of a nonmetric multidimensional scaling (NMDS) analysis. To maintain consistency in the distance metrics during comparison, chi-square distances based on plot-wise species abundances were used for the NMDS. As part of exploratory procedure for plot classification, we performed a hierarchical agglomerative clustering of the plot coordinates on the most prominent CA axes, using the Euclidian distance and Ward’s minimum variance criterion (Legendre & Legendre 1998). Complementary data on species phenology (Pascal 1986) were also used for ecologically meaningful categorization of these plot clusters. To assess uncertainty in the cluster delineation, we performed multiscale nonparametric bootstrap resampling tests (Shimodaira 2002, Suzuki & Shimodaira 2004), which helps to determine (through P-values) if a given cluster in the hierarchy has been designated by chance, due to sampling error.

Patterns in stand structural characteristics of the BSP were analyzed through a principal component analysis (PCA). The structural characteristics included two diversity variables (species richness [Sp] and Shannon index [Shan]), two floristic parameters (proportion of trees belonging to deciduous species [Dec] and number of species endemic to the WG region [End]) and three physiognomic variables (diameter of the tree of mean basal area [Dg] summarizing the within-plot distribution of diameters, canopy cover [CanoCov] and mean canopy height [CanoHt]).

Statistical analyses were performed using the ade4 (Chessel et al. 2004), labdsv (Roberts 2006), vegan (Oksanen et al. 2009) and pvclust (Suzuki & Shimodaira 2006) packages for R statistical software (http://cran.r-project.org/).

**RESULTS**

**Species Composition, Richness and Endemism.**—A total of 61,906 individuals, belonging to 400 plant species in 254 genera and 75 families were recorded from the 96 plots. These 400 species included 343 trees and shrubs, 56 woody climbers (lianas) and one strangler species. The density of trees in plots (≥ 10 cm gbh) was 98–1894 individuals/plot, with a mean of 645/ha. The range of number of species recorded was 14–96/ha (mean = 49 species). The families Euphorbiaceae, Rubiaceae, Lauraceae and Moraceae constituted 23.5 percent of total number of species recorded.

Of the 400 recorded species 33 (8.2%) occurred only once and 60 percent of the total number of individuals belonged to just 29 species. One hundred and thirty-five species (34%) had < 10 individuals recorded. The most common tree species were Terminalia paniculata (3811 individuals), Xylixylocarpa (3498), Olea dioica (2366) and Poeclioneuron indicum (2220). The maximum abundance in a single plot was observed for X. xylocarpa, with 730 individuals representing 75 percent of the plot density. Classification of the tree species based on the phenological characteristics showed that more than three quarters (309) were evergreen in nature, the remaining (91) being deciduous. Only six plant species were exotic, while ca 25 percent of the native species (97 of 394) were endemic to the WG, of which two were deciduous. Of these endemics, Bauhinia foveolata, Garcinia indica and Hopea canarensis are distributed only in the WG of Karnataka (Ramesh et al. 1997).
Floristic Analysis.—We performed a CA on the matrix of abundances of 400 species in 96 plots. The histogram of CA eigenvalues, when compared with a broken stick distribution (Legendre & Legendre 1998), showed seven significant axes of which the first three appeared highly prominent, accounting for ca 20 percent of the total variance (Fig. 2A). A three-dimensional representation revealed a strong nonlinear relationship between plots’ coordinates on these axes (Fig. 2B) indicating that the main floristic gradients in the region were not independent of each other. These axes correlated with the main bioclimatic variables in a complex way (Pearson’s \( r \) for sites’ scores along CA axes 1–3 are respectively \(-0.77, 0.36\) and 0.05 with rainfall; \(0.53, 0.37\) and \(-0.15\) with dry season length; \(-0.10, -0.52\) and \(-0.06\) with altitude, a proxy for minimum temperature), and the distribution of species along the CA gradient showed a progressive change in mixture of evergreen and deciduous species (Fig. 2C). The gradients observed in CA were similar to that of the NMDS (see supporting information Fig. S1), with significant correlation between the first axis of CA and NMDS (Pearson’s \( r = 0.77 \)). Both CA and NMDS show an arch-like pattern that suggests a coenocline and not just an artifact of the CA method. We then used a hierarchical clustering on plots’ scores along the three first CA axes for delineating groups of plots with homogeneous floristic composition. We found that splitting the plots into five different categories was ecologically meaningful, i.e., it allowed us to identify floristic groups that broadly reflected the major bioclimatic features of the region (Fig. 3).

The wet evergreen group 1 (WE1) corresponds to plots growing under very high rainfall (5620 ± 1757 mm/yr) with a short dry

![Figure 2](image-url)
season (4.4 ± 0.5 mo), and almost exclusively composed of evergreen species. The wet evergreen group 2 (WE2) represents plots under high rainfall (4927 ± 1281 mm/yr) with a longer dry season (5.8 ± 0.4 mo), and largely dominated by evergreen species (> 90% of trees). The semi-evergreen (SE) group represents plots growing in much lower rainfall conditions (2971 ± 1215 mm/yr; 6 ± 0 mo) in which evergreen species are still frequent (> 66% of trees), but mixed with deciduous species. The MD group represents plots found in the 2055 ± 904 mm/yr of rainfall with 5.8 ± 0.4 dry month regions, and in which the deciduous species largely dominate in number of individuals (87%) over the evergreen species. The DD group is found under low rainfall and long dry season (1066 ± 214 mm/yr; 6.3 ± 0.5 mo), and is mainly composed of deciduous species (> 90% of trees). A multiscale bootstrapping test indicated that the wettest (WE1 and WE2) and driest (DD) groups were quite robust (P < 0.05 with 1000 bootstrap resampling of 24, 48, 72 and 96 species vectors), while the remaining two transitional groups were uncertain (P = 0.12 and 0.26 for MD and SE, respectively). Floristic composition of these groups that expound the patterns observed in our data (Figs. 1, 2B and C) are described below.

WE1 is characterized by the presence of *P. indicum*, which is largely dominant in the plots of high elevation (> 900 m asl) near Kudremukh, where this species can represent up to 50 percent of the total number of trees (> 10 cm g/h). It is sometimes codominant with *Cleistanthus malabaricus* (e.g., Kudremukh region) or associated with *Dipterocarpus indicus*, particularly in the lower elevation plots (ca 600 m asl), yet under high rainfall, in Agumbe region (Fig. 1), where *P. indicum* represents ca 25 percent of the total number of trees. Depending on their degree of disturbance, plots belonging to WE2 can harbor some typical evergreen (*D. indicus*, *Persea macrantha*, *Diospyros* spp., *Holigarna* spp.) or secondary deciduous (*T. paniculata*, *Terminalia bellirica*) canopy species. But the most common species in these plots are subcanopy and understory evergreen species such as *Hopea ponga*, *Knema attenuata*, *O. dioica* or *Dimocarpus longan*. *Memecylon umbellatum* was also abundant in some plots of this group, as canopy and subcanopy trees, particularly in the northern part of the study area (around Anshi). In this group, one plot near Sorab receives less rainfall than the others (ca 1600 mm/yr) and represents a particular edaphic facies more common in SE. In SE, the evergreen species such as *Aporosa lindleyana*, *Flacourtia montana*, *O. dioica* and *Ixora brachiata* are mixed with deciduous species typical of the dry forests such as *T. paniculata* or *Lagerstroemia microcarpa* of secondary formations like *Tabernaemontana beyneana* or even of savanna vegetation like *Cattaneramum dumetorum*. However, within SE, there are two different subgroups that share a similar set of species, those especially evergreen. Those found under high rainfall (> 2000 mm/yr) correspond to the secondary stages of disturbed evergreen formations, while the ‘Kan forests’ (Pascal et al. 1988) particularly develop due to specific edaphic conditions near Sorab, within a range of rainfall of 1500–2000 mm/yr, where the evergreen forest cannot usually survive (Fig. 1).

A majority of the plots belonging to the MD group occur in the transition zone between the evergreen and deciduous domains, i.e., rainfall of 1500–2000 mm/yr. The canopy is generally dominated by *T. paniculata* and *T. tomentosa* along with *L. microcarpa* and *Dillenia pentagyna*, while various evergreen species occupy the subcanopy and understory layers. Some of the plots in this group (e.g., those around Yellapur) are, however, found in zones of higher rainfall (2500–4000 mm/yr), where they constitute secondary stages of highly disturbed evergreen forests where *Terminalia* spp. represent ca 37 percent of the trees. Other plots in which the *Terminalia* spp. constitute ca 43 percent of the total number of trees receive < 1500 mm/yr of rainfall in the Sorab region (Fig. 1), where they can be considered as degraded stages of the Kan forests. In some plots with ca 1500 mm rainfall and a long dry season (6–7 mo) near Bommanhalli in the northern part of the study area, *Tectona grandis* is a codominant canopy species in transitional formations toward DD forests. In this group, some plots dominated by the deciduous subcanopy species *X. xylocarpa*, which constitute > 60 percent of the total number of trees, represent highly disturbed secondary formations. The plots that belong to the DD group and receive > 900 mm rainfall are generally codominated by *T. paniculata*, *T. tomentosa*, *T. grandis* and *Anogeissus latifolia*, thus representing transitional stages toward MD formations (near Bommanhalli; Fig. 1). However, both *Terminalia* spp. are almost absent from the typical DD forest, which is largely dominated by *A. latifolia* representing up to 40 percent of the trees in some plots around Shimoga, where this species is found along with *Chloroxylon swietenia* and *Albizia amara*. A list of species that characterize each of the habitat types documented during the study is provided in supporting information Table S1.
STRUCTURAL ANALYSIS.—We performed a PCA on the matrix of the seven structural parameters in the 96 sampling plots. This analysis exhibited two prominent first axes accounting for 55 and 23 percent of the total inertia, respectively (Fig. S2). This analysis revealed that the diversity (Sps and Shan) and floristic characteristics (End and Dec) of plots vary orthogonally to the physiognomic characteristics (Dg, CanoCov and CanoHt). Indeed, the first PCA axis conforms to the floristic gradient revealed through CA (Pearson’s r with CA axes 1–3 are 0.82, −0.54 and −0.03, respectively), and segregated the evergreen plots sensu lato (i.e., WE1, WE2 and SE) from the deciduous ones (MD and DD), based on lower proportion of trees belonging to deciduous species (Dec), higher diversity measures (Sps and Shan) and higher number of endemic species (End) (Fig. S2).

The second PCA axis is positively correlated with the physiognomic parameters, canopy height (CanoHt), canopy cover (CanoCov) and mean tree diameter (Dg), and reveals the large variability of these variables within each of the floristic groups. This axis, however, does not correlate with CA axes (r with CA axes 1–3 are 0.16, −0.09 and −0.35, respectively), implying that the structural properties of the plots were not altogether related to their floristic composition. This also indicates that plots with similar floristic compositions can encompass contrasting physiognomic structures, probably as a consequence of the particular history of each plot regarding phases of habitat disturbance and recovery.

The distribution of plots of the five floristic groups with respect to rainfall, species richness and percentage canopy cover is provided in Figure 4A, while that of rainfall, percentage of deciduous trees (Dec) and the mean tree diameter (Dg) is given in Figure 4B. It shows a positive relationship between precipitation and species richness (diversity), with species richness in plots increasing along the rainfall gradient and across DD to WE types (Fig. 4A).

Also, in conformity to Pascal (1988), all DD plots are found <1500 mm rainfall, while the transitional domain (1500–2000 mm rainfall) contains either MD plots dominated by deciduous species with lower species richness or SE plots that correspond to the edaphic facies of the Kan forests as described by Pascal et al. (1988). At the opposite extreme, under very high rainfall (>5000 mm), evergreen plots (WE1 or WE2) never contained >20 percent of deciduous trees, even when the mean tree diameter and canopy cover was very low. Most SE and MD plots of 2000–3000 mm rainfall are located near Bommanhalli and Yellapur, in the northeastern part of the study area, where the dry season lasts 6–7 mo and probably limits many evergreen species. Many of these plots also exhibit very low mean tree diameter, as well as very low canopy cover, indicating they probably suffered high anthropogenic pressure. At 3000–5000 mm rainfall, however, evergreen (WE1, WE2), SE and MD plots displayed a large breadth of tree diameter and canopy cover illustrating the full range of floristic gradient of evergreen formations toward secondary SE and MD forests.

DISCUSSION

THE CENTRAL WG FORESTS OF KARNATAKA.—The central WG has been reported to be floristically less diverse, and with fewer endemic species than the forests in southern WG. Floristically, southern WG wet evergreen forests at low-medium elevation have high tree species richness (278–384 species found across this region) and endemism (44–65%) due to high topographic complexity and moderate length of dry season (2–4.5 mo; Pascal 1988, Ramesh 2001b, Davidar et al. 2005). In comparison in central WG, the lower tree species richness (69–278 species found across this region) and endemism (15–36%) could be attributed to a longer dry period (4–7 mo). The dominance of the families Euphorbiaceae and Rubiaceae observed during this study, however, is similar to the patterns observed across WG. There were broad similarities in the species composition of Pascal’s (1986) floristic types (derived mostly from undisturbed, climax forests) and that observed in our floristic groups. For example, species among the wet evergreen types D. indicus, P. indicum, Diospyros spp. and Memecylon spp., and among deciduous forests types, A. latifolia, L. microcarpa, T. grandis and D. pentagyna were also observed in our plots. The dominance of certain species, P. indicum, O. dioica, T. paniculata, X. xylocarpa and A. latifolia, however, clearly influenced our floristic group categorization.
The occurrence of forest stands dominated by few species, amidst high diversity forests, has been well documented in the literature (Connell & Lowman 1989, Hart et al. 1989, Torr & Lowman 1989). Torr & Lowman (1989) summarized the varied patterns of monodominance in the different regions of the tropics, with frequent occurrence in Africa, while being very few in Amazon. In Asia, although several species that form monodominant stands occur, dominance is more prevalent at the family level. In many of these forests, however, single tree species constitute > 90 percent of the total number of trees (see Hart et al. 1989 for comparison across the tropics). With regards to the central WG, monodominant stands of P. indicum (Kadambi 1942, Rai & Proctor 1989) have been reported from the South Bhadra region (close to Kudremukh) and in Kudremukh (Pascal 1988). During our study, although dominance of P. indicum was observed in Kudremukh region, this species constituted only about 50 percent of the total trees. While Terminalia spp. and A. latifolia represented about 40 percent of the total trees in some plots, X. xylocarpa was found to be more dominant in some plots, representing up to 75 percent of the trees. The percentage dominance of these species, however, was highly variable at different sites of the study area. The broad and varied patterns of the species distribution observed during this study broadly reflect the bioclimatic and disturbance (e.g., historical and present land uses) attributes of the study area.

Regional diversity patterns: Environmental correlates and disturbance history.—The regional variation in species abundance across central WG forests has been documented by this study, and a broad pattern of variation over bioclimatic gradients was observed. Based on our analyses, three major, well-delineated floristic groups were derived with well-defined relationships to mean annual rainfall. The wet evergreen groups (WE1 and WE2) occurred in high-rainfall regions (> 5000 mm/yr) and the DD group occurred in low-rainfall regions (< 1500 mm/yr). Exceptions to this are the Kan forests in the Sorab region, where rainfall is low (1500–2000 mm/yr) for the presence of evergreen forests that are comparable to wet evergreen forests at the same latitudes (Pascal et al. 1988). Edaphic characteristics where better soil water budget compensates for the low rainfall explains the maintenance of these evergreen forests (Bourgeon & Pascal 1989). The broad influence of rainfall on the regional floristic composition is thus evident. The intermediary rainfall zone (1500–5000 mm/yr), however, comprised of plots belonging to both evergreen and deciduous groups with a high variation in phenological traits.

At macroscales (entire WG), Davidar et al. (2007) reported that seasonality might drive wet evergreen forest beta diversity and at local scales rainfall could be influential. Our data suggest that, at regional (central WG) scale, alpha diversity is mainly related to the rainfall gradient. With regards to beta diversity, the influence of seasonality might be limited just to the wet evergreen forests (viz., high-rainfall zone) and other environmental factors (such as soil) might also play a role. In contrast to the areas with wet evergreen forests, in the plains of the central WG region with dry forests (viz., low rainfall) the difference between the lengths of dry period is not high. Hence, there is a marked difference in the patterns of beta diversity between wet evergreen forests (high beta diversity) and dry forests (low beta diversity).

In the wet evergreen forests of our study area, high beta diversity and varied patterns of species distribution were observed. P. indicum dominated or was observed in association with C. malabaricus in the WE1 group occurring in regions with 4–5 mo of dry period and at a higher altitude (ca 1000 m asl). P. indicum was observed in association with D. indicus in regions with a 5 mo dry period and lower altitude (ca 660 m asl), while Memecylon spp. dominated plots in WE2 were found in the northern extreme of the study area at regions with 5–7 mo of dry season. In the high-rainfall zone, the differentiation of the WE1 and WE2 observed in this study could be attributed to other bioclimatic parameters (dry season) or influence of soils. Plots dominated by Memecylon spp. are often found on lateritic out crops and either in the intermediate zone of Precambrian soils and Deccan traps or exclusively on the Deccan traps in the Anshi region. However, across the dry forest region (with low rainfall), the length of the dry season was high (6–7 mo) and not variable. Also, the beta diversity was low and was mostly dominated by A. latifolia.

Ramesh (2001b) suggested that in the wet evergreen forests, the effect of temperature is more pronounced in bringing out the dissimilarity among different floristic types than that of the more gradual duration of dry season. It should be noted, however, that the passage from one WG forest type to another is not abrupt. A phenomenon also observed in our study, with variations within the floristic groups, and particularly mixed patterns at the intermediary rainfall zone (2000–5000 mm/yr) where both evergreen and deciduous forests occur. Although the floristic composition broadly follows a rainfall gradient, the distribution patterns within them are not clearly defined along any environmental gradient especially in the intermediate rainfall zone. The differences could be due to the heterogeneity in the environmental, edaphic and microclimatic conditions brought by the WG relief in short spatial areal extent. Lack of clear floristic patterns could also have been brought about because of forest disturbances. The PCA elucidated the differences in the structural attributes within each of the floristic groups, a result of varying intensity of disturbance. This variation in stand structure within the main floristic types also reveals the effects of disturbances on the floristic composition.

The intermediate rainfall zone with predominant areas in the Malnad region and central WG in general, has had a long history of ecological disturbances since Paleolithic period (Chandran 1997). Based on palynological investigation, Catatini et al. (1991) documented a change in vegetation in Uttara Kannada region 3500 BP, with reduction in evergreen and deciduous species and an increase in savanna species. In the past this region has been subjected to agro-pastoralism (3000 BP), shifting cultivation (2000 BP) and slash and burn agriculture (prevalent till ca 1000 BP; Chandran 1997). Slash and burn agriculture (Khumri) continued till recently, regulated and controlled by the British Empire (Buchy 1996). During the colonial period a large extent of the hardwood species (Poecloloneuron spp., Calophyllum spp. and Hopea spp.) were removed for electric poles and railway sleepers (Stracey 1959, Nadkarni 1989). The ‘selective’ logging, which was in force until 1986, contributed
to altering the biomass and floristic diversity in the forests. According to Karnataka forest statistics (1984), 173,846 m$^3$ of rosewood ($Dalbergia latifolia$), teakwood ($T. grandis$), other timbers ($Anogeissus spp.$, $Lagerstroemia spp.$, and $Terminalia spp.$), plywood ($Dipterocarpus spp.$, $Vateria spp.$) and firewood was extracted between 1976 and 1985. Nonsustainable harvesting of non timber forest produce has also affected the regeneration and population structure of several economically and medicinally important species including endemics like $G. indica$ and $Myristica malabarica$ (Ramesh et al. 2009b). Further, natural forests were cleared for forestry practices involving monoculture plantations and conversion to other cash crops plantations like ‘areca’ (Buchy 1996). For a unit of areca planted, owners are allotted 8–10 units of forest area (‘betta lands) to clear understory and collect litter to use as crop mulch (Nadkarni 1989). Many reservoirs have also been built across the rivers in the central WG. These various past and ongoing disturbances have not only contributed to loss and degradation of forests but also impacted the floristic composition (Ramesh et al. 2009a).

Our data suggest that the responses of the plant species to these disturbances could be varied, depending on the climatic constraints on them. For example, in the high-rainfall region, these disturbances may not promote the invasion of deciduous species and only evergreen floristic groups are found. Similarly, in the low-rainfall zone, disturbance only resulted in changes in relative percentage of deciduous species. Hence, the grouping of the sampling plots into floristic categories (WE1, WE2 and DD) was robust, as indicated by the multiscale bootstrapping test. In the intermediate rainfall zone (which is also potential evergreen zone, with rainfall of 2000–5000 mm/yr), however, the proportion of deciduous species in plots is a good indicator of disturbance. The gradual increase in the proportion of deciduous species from WE2 to SE (except Kan) and MD in this zone indicates an increase in the secondary nature of stands. This trend of overlapping evergreen and deciduous species occurring in varied transient forest stages could be the reason for the uncertain categorization for the MD and SE floristic groups.

Explaining the species composition and defining vegetation zones based on quantitative inventories of tropical forests are difficult due to the high species diversity, many unpredictable features, drift and chaos (Condit 1996). This study has described the mesoscale patterns in floristic composition of central WG, broadly relating the floristic groups and species therein to the environmental gradient, namely rainfall. Accurate identification of the environmental disturbance correlates of the floristic composition and abundance of tree species observed in this study is beyond the scope of this paper and further detailed investigations are being carried out.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**TABLE S1.** List of characteristic species for each of the forest types documented during the study in central Western Ghats region of Karnataka, India.

**FIGURE S1.** Similarity of gradients in correspondence analysis and nonmetric multidimensional scaling performed on the abundance matrix of 400 woody species in ninety-six 1-ha plots in the central Western Ghats of Karnataka, India.

**FIGURE S2.** Principal component analysis conducted on seven structural parameters at ninety-six 1-ha plots in the central Western Ghats region of Karnataka, India.

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