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Spatial Patterns of Phytodiversity - Assessing Vegetation Using (Dis) Similarity Measures

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1. Introduction

Patterns in vegetation can be expressed through the variation in species composition between plots, which has been termed 'beta-diversity' by Whittaker (1960, 1972). The general importance of beta-diversity has been emphasized in recent years (e.g. Gering et al., 2003; Olden et al., 2006; Sax and Gaines 2003; Srivastava 2002). However, even though Legendre et al., (2005) postulate that "beta diversity is a key concept for understanding the functioning of ecosystems, for the conservation of biodiversity, and for ecosystem management", implementation is still scarce compared to measures of species richness, alpha-diversity and its derivatives (but see e.g. Condit et al., 2002; Kluth and Bruehlheide, 2004; Pitkänen 2000).

However, the term 'beta-diversity' is not very clear and has multiple meanings (e.g. Jurasinski and Retzer, 2009; Lande, 1996; Qian et al., 2005). Most often 'beta-diversity' is defined as the compositional similarity between vegetation samples (sites, habitats, plots) expressed through (dis)similarity or distance measures. Generally, compositional similarity decreases with distance between plots. This phenomenon is called 'distance decay' of similarity (Tobler, 1970) and can be seen as a characteristic of all geographic systems. Nekola and White (1999) investigated species compositional similarity between fir and spruce stands across North America (Qian et al., 1998, 2005) and concluded that distance decay of similarity might be useful as a descriptor of diversity distribution as well as for the study of factors influencing the spatial structures of communities. The few comparative studies investigating distance decay for more than one group of organisms show that it heavily depends on organism groups as well as on the region under study (Ferrier et al., 1999; Oliver et al., 2004).

Although it is far from being well covered, the spatial change in species composition has received some more attention in recent years (Jurasinski and Retzer 2009). The phenomenon

was utilized to evaluate the validity of the dispersal theory (Hubbell 2001) against niche concepts in the Neotropic: Chust et al., (2006), Condit et al., (2002), Duivenvoorden et al., (2002) and Ruokolainen et al., (2002), investigated distance decay in terra firme forests in Panama, Ecuador, and Peru, whereas Duivenvoorden et al., (1995), Ruokolainen et al., (1997), and Tuomisto et al., (2003) concentrated on rain forests in the Amazon basin. However, there are no studies in this regard in the Paleotropic. This hinders the overall generalization of the findings. The data set of the Eastern Ghats provides a unique opportunity as we can calculate distance decay rates in paleotropic ecosystems. Unfortunately there were only few environmental variables recorded. Furthermore these are categorical and assign relatively coarse classes to the plots.

Our aim is to develop a spatially explicit, widely applicable method to assess phytodiversity encompassing species richness, spatial and temporal heterogeneity, and functional diversity and to relate it to environmental conditions (including site conditions, disturbance regime and biological richness value). There is an urgent need for standardized and comparable data in order to detect changes of biodiversity. Such methods are required to be representative as well as pragmatic due to the simple fact that there is insufficient time to obtain complete data sets relating to temporal trends. If biodiversity is lost rapidly at the landscape level, frequent re-investigations have to be done in order to detect and analyze such changes. Thus, our objective was to provide a method that allows for the tracking of changes in biodiversity at the landscape scale. Here, we investigate the distance decay of compositional similarity whilst accounting for the change of the relationship between compositional similarity and its drivers with geographical distance between plots.

Steinitz et al., (2006) highlight that the studies are limited to which extent patterns of distance decay depend on the position along environmental gradients. Accordingly Jones et al., (2006) emphasize that explanatory power of variables might increase with the length of the gradient covered. Based on this, we hypothesize for the present study (Eastern Ghats part of Andhra Pradesh, India) as:

1. Similarity in plant species composition decreases continuously with distance. Due to the small scale of the study (largest geographical distance covered is 8 km) the rate of distance decay will be relatively low compared to large-scale studies.
2. The correlation between compositional similarity of vegetation and the dissimilarity of predictor variables (vegetation type, disturbance - biological richness value, abiotic environmental conditions) is changing with geographical distance between multiple plots. We expect the correlation to increase with spatial scale/distance between sampling units because the sampled environmental gradient is likely to increase as well.
3. Disturbance is the main driver of vegetation patterns in the regarded transitional ecosystem. We especially consider disturbances because deciduous ecosystems of the Eastern Ghats have a long-lasting disturbance history and stress tolerators are clearly favoured compared to competitors (Rawat, 1997).

1.1 Previous studies

1.1.1 Measuring and analyzing similarity

Compositional similarity or differentiation diversity between sampling plots is an important basis for most numerical analyses in vegetation ecology. It is at the heart of ordination methods and has general importance regarding the testing of ecological theory (Legendre et al., 2005). Moreover, it represents the basis for most of the analyses in the present study and

shall therefore be discussed in some detail in this chapter. Data on species composition is generally of multivariate character. Thus, hypothesis testing regarding the relation between species composition and its drivers can hardly be achieved with normal statistics. This led to a specific set of methods for vegetation ecologists (Jongman et al., 1987; Legendre & Legendre, 1998; Leyer and Wesche 2007; Sokal and Rohlf, 1981). The majority of this method is based on the calculation of biological resemblance and ecological distance in data space. Resemblance can be calculated with a wide range of coefficients and indices, measuring similarity, dissimilarity, proximity, distance, association or correlation (Orlóci 1978; Tamas et al., 2001).

1.1.2 Measuring similarity

Compositional similarity measures differentiation diversity (Jurasinski and Retzer, 2009) and can be calculated with resemblance measures. These are available in two primary groups (Legendre and Legendre 1998): (1) Quantitative or distance indices are used to calculate the proximity of two samples in data space from quantitative measurements or abundance data. (2) Similarity/Dissimilarity measures can handle binary data as it is typically found in presence/absence data sets. There are a large number of different indices and coefficients available and comparative reviews can be found in Cheetham and Hazel (1969), Hubalek (1982), Janson and Vegelius (1981), Koleff et al., (2003), Shi (1993) and Wolda (1981). All binary similarity/dissimilarity measures are based on the same set of variables. Whether a coefficient measures similarity or dissimilarity depends on the implementation of the formula. However, most of them can easily be transformed from a similarity to a dissimilarity measure by calculating $1-S$ (with S being similarity, Legendre and Legendre, 1998; Shi, 1993). From some similarity coefficients a dissimilarity measure following the Euclidean metric can be obtained by calculating $\sqrt{1 - S}$ instead (for details see Legendre and Legendre, 1998).

Indices incorporating the species not present in both of the compared samples (d , see Fig. 1) are controversially discussed (e.g. Simple Matching by Sokal & Michener (1958) or the coefficient of Russel and Rao (1940)). Legendre and Legendre (1998) call these symmetrical (see Janson and Vegelius, 1981 for another definition of symmetry) and discuss the “double-zero problem” at the beginning of their chapter on similarity indices, because it “is so fundamental with ecological data” (Legendre and Legendre, 1998, p. 253): Species are supposed to have unimodal distributions along environmental gradients. If a species is absent from two compared sampling units (which is expressed by zeros in the species matrix), it is not discernable on which end of the gradient the both sites are with respect to a certain environmental parameter (Field, 1969). Both might be above the optimal niche value for that species, or both below, or on opposite tails of the gradient. Thus, the incorporation of unshared species (d) might lead to wrong conclusions when the relation between environment and species composition is under study (Legendre and Legendre, 1998).

Additionally, Shi (1993) states that the status of d in similarity coefficients for paleoecological studies is not clear and cannot be assessed directly because of its great dependence on the less common taxa absent from both sites: “In palaeontology, absence of a taxon, particularly a rare one, may have been derived from differential preservation and/or sampling errors rather than some ecological factors”. Finally, Field (1969) shall be cited as he found a very well fitting metaphor: “No marine ecologist would say that the intertidal and abyssal faunas were similar because both lacked the species found on the continental shelf”.

Fig. 1. Illustration of the matching components providing the basis for binary similarity measures a) the number of species shared by two compared units, b) the number of species unique to one of the compared plots, c) the number of species unique to the other one of the compared plots, d) the number of species not found in the two compared plots but in the whole dataset (unshared species).

(Dis) similarity indices, which take unshared species into account, mingle different ideas of differentiation diversity (additive partitioning, multiplicative partitioning, turnover, see Jurasinski, 2007). Furthermore, they tend to be less specific as the values show less variance because d is far bigger than a , b , or c for most of the datasets recorded in the field. “Including double-zeros in the comparison between sites would result in high values of similarity for the many pairs of sites holding only a few species; this would not reflect the situation adequately” (Legendre and Legendre, 1998). Furthermore is the total inventory diversity (gamma) as a background for the calculation of d often difficult to define. When temporal changes are addressed, the question arises, whether the species pool of one time step or the whole species pool as recorded over several time steps should be regarded.

1.1.3 Required features for a (Dis) similarity measures

From the previous studies mentioned above it is obvious that a measure of diversity should possess the following three properties:

- It compares the similarity of a focal plot to several other plots, e.g. its surrounding neighbors taking species identity into account.
- It yields a single value as result, which can be directly attributed to the investigated focal plot.
- Its values should range between 0 and 1 for the sake of standardization and ease of interpretation.

From the multi-plot similarity measures found in the literature and introduced above, none meets all these properties. Thus, we propose a new multi-plot similarity measure, which is discussed in the method section. We call it simply the coefficient of multi-plot similarity. The performance of this new measure regarding the detection of typical pattern is tested for the random and continuous datasets carried out in the Eastern Ghats of Andhra Pradesh (India).

2. Materials and methods

2.1 Study site

957 random plots spread across Eastern Ghats of Andhra Pradesh were used in this study (Fig. 2). To typify the Eastern Ghats of Andhra Pradesh at landscape level it was classified in

two zones viz., northern Eastern Ghats (Zone-1) and southern Eastern Ghats (Zone-2). Following the gradient in the geology, soil, bioclimatic (temperature and precipitation), altitude and degree of disturbance, the zones were characterized and analysed. For continuous enumeration a total of six transects were laid and data collected was used for analysis. These transects were laid both in zone-1 and zone-2 and distributed evenly in deciduous ecosystems.

Fig. 2. Location map of the six transects and zones of the northern and southern Eastern Ghats for random plots in the state of Andhra Pradesh, India

The areas studied are three 0.5-ha plots, which are located in the Sileru-Maredumilli ranges of the Northern Eastern Ghats of Andhra Pradesh (zone-1) and Nallamalais-Seshachalam-Nigidi hill ranges of Southern Eastern Ghats of Andhra Pradesh (zone-2) (Fig. 2). These forests are classified as South Indian Moist Deciduous and Orissa Semi evergreen forests (Champion & Seth, 1968). Three 0.5ha plots area was established at three different sites: Site 1 is located about 2 km from Sukkumamidi, a tribal hamlet in Khammam district, which receives mean annual rainfall about 1200-1400mm and elevation ranging from 400-600m. Site 2 is located about 6 km from Maredumilli tribal village in East Godavari district, receives mean annual rainfall about 1400-1600mm with an elevation of 600-800m. Site 3 is located about 2 km from Lankapakala tribal hamlet in Visakhapatnam district receives mean annual rainfall 1600-1800mm and an elevation of 800-1100m is shown in Table 1. All the three study sites were undisturbed. There are no records on the intensity and the extent of disturbance.

The next set of sample plots were laid in Southern Eastern of Andhra Pradesh (zone-2). These forests are classified as Tropical Dry Deciduous by Champion & Seth (1968). Three 0.5ha plots area were established at three different sites: Site 4 is located about 3km from

Peddacheruvu, a chenchu tribal hamlet in Nallamalais of Kurnool district which receives mean annual rainfall about 900-1000mm. Site 5 is located about 4km from Talakona, a Yanadi tribal hamlet in Seshachalam hills of Chittoor district which receives mean annual rainfall 800-900mm. Site 6 is located about 2km from Kuntlapalli village, Anantapur district receives mean annual rainfall about 600-700mm. The rocks are of Kurnool-Cuddapah formations (quartzite and slate formation predominate) and altitude ranges from 400-600m. Thus, these sites show variability in rainfall pattern even though phytogeographical range is contiguous.

Sites	Location	Forest type	Elevation (m)	Rainfall (mm)
1	Sukkumamidi	Moist Deciduous	500	1200-1400
2	Maredumulli	Moist Deciduous	700	1400-1600
3	Lankapakala	Moist Deciduous - Semievergreen	900	1600-1800
4	Peddacheruvu	Dry Deciduous	600	900-1000
5	Talakona	Dry Deciduous	700	800-900
6	Kuntlapalli	Dry Deciduous	800	400-600

Table 1. Study area detail for the continuous plots on its forest type, elevation and rainfall pattern in Northern and Southern Eastern Ghats of Andhra Pradesh, India

2.1.1 Geographical extent

The Eastern Ghats are a discontinuous range of mountains along eastern coast of Peninsular India extending over 1750 km with the average width of about 100 km and extends from 10°05' to 22°30' N Latitude and 76°23' to 86°50' E longitude (Fig. 2). The Eastern Ghats are 'tors' of geological antiquity and are geologically older than Himalayas and Western Ghats. Eastern Ghats cover four states (Orissa, Andhra Pradesh, Tamil Nadu and small portion of Karnataka) and present study was undertaken in the Eastern Ghats part of Andhra Pradesh lying approximately between 12 – 19 N latitude and 76 – 84 E longitudes. It is bounded by Eastern coast on the East, Deccan plateau on the West, South and North covers the Eastern Ghats part of Tamil Nadu and Orissa state respectively. Study area includes Eastern Ghats districts of Andhra Pradesh viz., parts of Srikakulam, Vizianagaram, Visakhapatnam, East Godavari, West Godavari, Khammam, Krishna, Mehbubnagar, Nalgonda, Guntur, Kurnool, Anantapur, Prakasam, Kadapa, Nellore and Chittoor (Fig. 2). The total geographical area covered under Eastern Ghats of Andhra Pradesh is 98,662 km² having 23,894 km² of forest area. Major rivers like Godavari, Krishna and Pennar cut the range into discontinuous blocks of hills along the East coast in Andhra Pradesh. Major forest range includes the Upper Sileru range in north, lower Velikonda Range lies to the east, and the higher Palikonda-Lankamalla-Nallamalla ranges in the west. Eastern Ghats also harbours wide range of wild crops (millet, rice) and economic and medicinal plants. Endemic plants of this region are basically Palaeo-endemics and are localized. They have very narrow distribution range and several studies indicate that they are under gradual process of extinction (Reddy et al., 2006). Nearly, 54 tribal communities

inhabit Eastern Ghats region (MoEF, 1997). The Eastern Ghats also harbours one of the richest Bauxite deposits in the world.

2.1.2 Vegetation distribution

Andhra Pradesh ranks first amongst the states and Union Territories in terms of area under tree cover (SFR, 2001). The total forest area of the state is 44,637 km², which occupies 16% of the total geographical area of 2,75,068 km² (SFR, 2001). The forests in the region are broadly classified into Semi Evergreen, Moist Deciduous, Dry Deciduous, Thorn and Scrub forests and are comparable with the existing (Champion & Seth, 1968) classification.

2.1.3 Geology, Soil and bioclimate

Eastern Ghats is not formed of one particular geological formation but consist of rocks varying in origin and structure according to the location. Geologically, zone-1 is mainly of Charnockites and Khondalites (Krishnan, 1960) having red and black soil, while, zone-2 is made up of Quartzite and Slate formations with red, mixed red, black and lateritic soil.

Climate of zone-1 is warm and humid with an annual precipitation of 1200-1700 mm compared to zone-2 which is hot and dry with lesser precipitation of 600-1000 mm. Topographically, zone-1 has higher altitudinal range (100-1672m) compared to zone-2 (100-1000m).

2.1.4 Protected area

Eastern Ghats of Andhra Pradesh has 1 National Park (i.e., Sri Venkateshwara National Park) and 6 wildlife sanctuaries (viz., Papikonda Wild Life Sanctuary (WLS), Kolleru WLS, Nagarjunsagar Srisailem Tiger Reserve (NSTR) WLS, Gundla Brahmeshwarm WLS, Sri Lankamalleshwara WLS and Sri Penunsila Narsimha WLS) of these only Kolleru WLS is the largest fresh water lake in the country and also treated as one of the Ramsar convention wetland sites in the world.

2.2 Methodology

2.2.1 Phytosociology data analysis

For the analysis of data the methodology is same as discussed in chapter-2. Six transects were laid (10 x 500m) and the individuals with ≥ 10 cm were enumerated. For each of these plots the GPS location was collected using handheld Garmin E-trex GPS and other biotic and abiotic environmental parameters (slope, aspect and altitude) were gathered. The fieldwork was conducted in January 2006 to March 2007.

2.2.2 General considerations for statistical analysis

For evaluating distance decay relationships one basically plots similarity between sites against their geographical distance (Nekola & White, 1999). So the first to calculate are similarities between sample locations. There exists a multitude of coefficients for the calculation of compositional resemblance of species samples.

Sørensen similarity (Sørensen, 1948) is used to calculate compositional similarity based on plot inventories of all tree species throughout the presented study. Sørensen similarity does satisfy the criteria of linearity, homogeneity (if all values are multiplied by the same factor the value is not changing), symmetry (independence from calculation direction, after (Janson and Vegelius, 1981) and scaling between 0 and 1 (Koleff et al., 2003). It is well

established and extensively used especially in vegetation ecology (e.g. Condit et al., 2002; Kluth & Bruelheide, 2004). This guarantees comparability with other studies. Sørensen is favored over Jaccard because the latter is more important in zoological studies (Koleff et al., 2003). Sørensen differs insofar that it does weight the shared species double which is seen as advantageous by Legendre & Legendre (1998) since shared species have more explanatory power regarding the underlying processes of the found patterns (Watt, 1947). Geographic distances between plots were obtained through the calculation of Euclidean distances between the x- and y-coordinates with the function `dist()` of the R package base (R Development Core Team, 2005).

2.2.3 Slope and aspect

Slope aspect and slope inclination may have a significant effect on species richness (Badano et al., 2005) and species composition especially in semi-arid vegetation (Sternberg & Shoshany, 2001). To obtain a distance measure integrating aspect and inclination, we use the model of a unit sphere and calculate great-circle distances between virtual locations. This allows for the generation of continuous rather than class variables as e.g. found in Kjällgren and Kullman (1998). For each plot a virtual location on the sphere is defined using the values for aspect as longitude and 90°-inclination as latitude. Therefore the virtual points are located in the pole region as long as inclination is low which leads to small (virtual) distances between them. The idea behind is that solar radiation; wind or other factors highly depending on aspect and inclination (Wilkinson & Humphreys, 2006) are not considerably different on plots with varying aspects as long as inclination is low. The longitude values on the unit sphere are derived from the directional reference made in the field. The equator of the sphere is thought as the compass circle. The Prime Meridian of the virtual sphere is the great circle through North and South of the compass. As in geographic terms longitude counts positive in Eastern and negative in Western direction. With Φ = latitude = 90°-inclination and Λ = longitude = aspect the great circle distance between A and B can be calculated with formula 1. As we use a unit sphere the maximum distance between two inclination/aspect pairs is perimeter/2 of the sphere, which is by definition π . To scale the possible distances between 0 and 1 the results of formula [1] are divided by π . Thus, a great-circle distance of 1 is rather scarce in the real world; however, two vertical rock walls with opposite aspect would share it.

$$\zeta = \arccos(\sin(\phi_A) \cdot \sin(\phi_B) + \cos(\phi_A) \cdot \cos(\phi_B) \cdot \cos(\lambda_B - \lambda_A)) \quad (1)$$

2.2.4 Statistical analysis

All statistical analyses were performed using functions of the packages base, stats, vegan and simba of the R statistics system (R Development Core Team, 2005). For better reading it is referred to the functions in the form 'function [package]' when the package is not mentioned before or 'function ()' when it is clear which package is meant in the following.

2.2.5 Compositional similarity

A common way to evaluate the structuring of compositional similarity within a data set is to use NMDS (Non-Metric multidimensional Scaling) plots. Non-metric multidimensional scaling (Kruskal, 1964) differs from other known ordination methods in that it does not build on a specific distance measure. Whereas PCA (principal components analysis), RDA

(redundancy analysis) rely on Euclidean distance, and DCA (detrended correspondence analysis), CA (correspondence analysis), CCA (canonical correspondence analysis) rely on ChiSquare distance, NMDS (as well as PCoA - principal coordinates analysis) is open to any kind of distance measure. Therefore it allows the implementation of measures, which have been proven adequate for ecological data as Bray-Curtis distance (Faith et al., 1987; Minchin, 1989). A good dissimilarity measure for communities has a good rank order relation to distance along environmental gradients. Because NMDS uses only rank information and maps these ranks non-linearly onto ordination space, it can handle non-linear species responses of any shape and effectively and robustly find the underlying gradients (Oksanen, 2005). It is an iterative ordination method that attempts to minimize a stress function, which measures the difference between the original floristic distances among sampling units and their new distances in the ordination space. Since NMDS is a non-metric method, it optimizes the rank order of distances rather than their actual values (Legendre & Legendre, 1998).

NMDS has been shown to be a very robust method regarding its reliability even when certain assumptions (like Gaussian species responses or sampling pattern) are violated (Minchin, 1989). NMDS was able to deal with any kind of response model, which was not the case for its strongest competitor, the DCA (ibid.). On the other hand the scaling of the axis scores does not allow drawing any conclusions regarding the position on the axis and ecological implications thereof. However, the positioning of sampled sites in a NMDS plot allows interpretation regarding their neighbors. These are similar in their species composition. When sites occur clumped in the NMDS this might be attributable to specific geographic positions or environmental conditions.

DCA bases on CA, which can be seen as a weighted principal coordinates analysis (PCoA), computed on ChiSquare distances (Faith et al., 1987). It therefore depends on the relationship between ChiSquare distance and ecological distance. This is the most important difference between the two methods: DCA is based on an underlying model of species distributions, the unimodal model, while NMDS is not. However, not all species exhibit the same response curve (e.g. Gaussian responses) (Minchin, 1989). Thus, it is preferable to use NMDS especially with no specific hypothesis regarding species environment interaction in mind. Furthermore Legendre & Legendre (1998) state that detrending should be avoided, except for the specific purpose of estimating the lengths of gradients. De'ath (1999) formulates that there are two classes of ordination methods - 'species composition representation' (e.g. NMDS) and 'gradient analysis' (e.g. the various flavors of CA). This means that NMDS rather is a mapping method, which allows for projecting the multi-variate data-space onto a two-dimensional map whereas PCA, CA and its relatives base on projection and rotation (Oksanen, 2004).

In the present case the alteration of species composition through time was in focus and not the gradient representation in species composition. Therefore NMDS is the method of choice as it furthermore enabled the use of Bray-Curtis distance which is the quantitative one-complement of the Sørensen index. Thus, the results are easily comparable and interpretation may not be hindered due to the implementation of different metrics.

2.2.6 Distance decay

Distance decay or spatial auto-correlation of quantitative univariate variables is usually calculated using semi-variograms (Legendre & Legendre, 1998). For multivariate data Mantel correlograms can be applied (Legendre & Legendre 1998; Sokal & Rohlf 1981). A simple

possibility for vegetation data is to regress similarity of units regarding species composition against their geographical separation (Nekola and White, 1999; Steinitz et al., 2006). To test for the influence of different vegetation types on patterns of compositional similarity data was divided into subsets. As the plots can be assigned to 2 geographically distinct regions, the distance decay of different vegetation types and subsets based on other categorical variables (fragmentation, slope, disturbance, etc.) is compared between the two regions.

The similarity values of the subsets are compared with an ANOVA-like function (`mrpp[vegan]`), (Oksanen et al., 2007)) and tested for significant differences using a permutation procedure (`diffmean[simba]`). Normal tests and ANOVA might fail here because the similarities are not independent from each other.

The Multiple Response Permutation Procedure (`mrpp`) allows testing whether there is significant difference between two or more groups of sampling units. The method is insofar similar to anova, in that it compares dissimilarities within and among groups. If two groups of sampling units are really different (e.g. in their species composition), then average within-group compositional dissimilarities ought to be less than the average of the dissimilarities between two random collections of sampling units drawn from the entire population. The `mrpp` statistic delta gives the overall weighted mean of within-group means of the pairwise dissimilarities among sampling units. The `mrpp[vegan]` algorithm first computes all pairwise distances in the entire dataset, then calculates delta. Then the sampling units and their associated pairwise distances are permuted, and delta is recalculated based on the permuted data. The last steps are repeated N times. N defaults to 1000 which provides a possible significance-level of $p < 0.001$ as significance is tested against the distribution of the permuted deltas.

After testing for significant differences between subsets, the differences in mean similarity are tested with a permutation procedure (`diffmean[simba]`). The difference in mean similarity between two sets is calculated. The two sets are joined together and two random sets the same size as the original sets are selected and their difference in mean is calculated. Then the sampling units and their associated pairwise distances are permuted, and the difference in mean is recalculated based on the permuted data. The last steps are repeated N times. N defaults to 1000 which provides a possible significance-level of $p < 0.001$ as significance is tested against the distribution of the permuted values.

To answer the question if distance decay is significantly different between the various evaluated subsets of the data, the slopes of the distance decay relationship have been calculated for the three subsets and compared. A permutation procedure following Nekola & White (1999) has been implemented as an R function (`diffslope[simba]`) to test for significance. For each subset compositional similarity between plots is regressed against their geographical separation. Before calculating the difference in slope between two subsets the values of compositional similarity are rescaled to a common mean. So testing the difference in slope of the distance decay relationship is independent of differences in the mean (Nekola & White, 1999; Steinitz et al., 2006). Linear regression is carried out on both of the subsets, and the difference in slope is calculated and stored. Then the variable pairs (geographical separation, compositional similarity) are randomly reassigned to the two data-subsets. Regression is calculated for each of the random subsets and the difference in slope is obtained again. The last steps are repeated 1000 times. Finally the difference between the observed slopes is compared to the differences based on random reassignment. Number of times when randomization are being produced differences in slope which is higher than the original data are summed up and divided by the number of permutations to get a p-value.

3. Results

3.1 Phytosociology analysis
3.1.1 Tree species richness and diversity indices

Results on the phytosociological parameters for the random plots are presented in Table 2. A total of 278 (zone-1) and 679 plots (zone-2) covering major vegetation types were enumerated to assess species richness, composition and diversity patterns. A sum of 25,621 individuals belonging to 963 species, 512 genera and 133 families were observed in the entire study area. It was observed that species richness was higher in zone-2 with 818 species belonging to 124 families as compared to 372 species of 95 families in zone-1. Herb species richness in zone-2 (350) was higher than in zone-1 having 101 species (Table 2). A total of 57 grass species majority of which belong to Poaceae followed by Cyperaceae were observed in this study.

Site	Vegetation type	No. of Plots	Trees	Shrubs	Herbs	Climbers	Grass	Species Richness	No. of tree Individuals	Families	Species Diversity (H')	Stand Density (ha ⁻¹)	Basal Area (m ² /ha)
Northern Eastern ghats (Zone-1)	Semievergreen	18	68	18	31	12	3	148	299	58	5.3	415.3	40.95
	Moist Deciduous	77	76	31	66	20	7	227	794	69	5.2	257.8	15.79
	Dry Deciduous	108	84	30	70	27	6	240	2100	75	5.0	486.1	19.04
	Dry Evergreen	17	52	17	37	12		135	181	57	5.2	266.2	8.65
	Thorn Forest	10	17	14	27	12	1	100	50	60	3.7	156.3	2.89
	Degraded Forest	48	64	19	44	18	4	165	863	59	4.2	449.5	12.94
	Total	278	137	51	101	44	10	372	4287	95			17.39
Southern Eastern Ghats (Zone-2)	Moist Deciduous	102	167	71	184	61	22	520	1511	104	6.6	370.3	13.28
	Dry Deciduous	325	191	87	281	73	37	680	5024	117	6.6	386.5	14.67
	Hardwickia Mixed	85	145	73	166	51	21	466	952	103	6.1	290.2	11.13
	Red Sanders Mixed	65	118	62	157	52	15	415	937	93	5.9	360.4	12.64
	Dry Evergreen	47	125	46	128	39	15	365	629	88	6.2	334.6	11.10
	Thorn Forest	36	112	55	93	48	11	326	427	86	5.7	296.5	8.61
	Degraded Forest	19	106	36	66	21	11	247	235	75	6.2	309.2	10.45
	Total	679	205	119	339	90	51	818	9715	124			13.15

Table 2. Species Richness in different vegetation type and habits in Northern and Southern Eastern Ghats of Andhra Pradesh, India

Parameters	Site					
	1	2	3	4	5	6
No. of Species	43	65	72	53	61	55
No. of Individuals	308	525	495	407	307	415
No. of Families	24	33	39	27	30	35
No. of Genera	37	59	61	46	54	48
Species Diversity	2.9	3.0	3.5	3.3	3.6	3.4
Basal area (m ² /ha)	14.71	17.61	24.42	4.35	10.11	6.82
No. of Endemics	2	0	0	1	0	138
No. of RET	0	0	4	9	2	2
Stand Density (ha ⁻¹)	616	1050	990	814	614	830

Table 3. Consolidated results for the six transect sites in Northern and Southern Eastern Ghats of Andhra Pradesh, India

For the six transects in both the zones results are presented in Table 3. A total of 6 transect of 0.5ha covering major vegetation types were enumerated to assess species richness, species composition and species diversity patterns. A total of 2,457 individuals belonging to 197 species, 139 genera and 57 families were observed in the entire study area. It was observed that species richness was higher in site 3 with 72 species belonging to 39 families as compared to other sites (Table 3). Least species diversity was found in site 1 and highest in site 5.

3.1.2 Species density, dominance, rarity

The first ten dominant species explains the dominance and structure of the forests. In zone-1, semi-evergreen forests are predominated by *Mangifera indica* (40.15), *Garuga pinnata* (15.98), *Xylia xylocarpa* (15.39) and *Stereospermum suaveolens* (15.38) (Table 4a) and this forest type doesn't exist in zone-2. In the case of Moist deciduous forests of the zone-1, it was represented by *Terminalia alata* (39.99), *Xylia xylocarpa* (22.22), *Pterospermum xylocarpum* (19.26) and *Bursera serrata* (9.15). Contrastingly zone-2 was characterized by *Limonia acidissima* (10.47), *Cassia fistula* (10.15), *Terminalia alata* (9.42) and *Madhuca indica* (7.28). Deciduous forest are the dominated forests among all the forest type, which is composed of *Xylia xylocarpa* (45.89), *Anogeissus latifolia* (24.48), *Terminalia alata* (12.42) and *Stereospermum suaveolens* (11.71) in zone-1, while in zone-2 *Chloroxylon swietenia* (14.83), *Anogeissus latifolia* (9.50), *Cochlospermum religiosum* (9.27) and *Sterculia urens* (8.15) dominates. The difference in species composition is mainly due to the variations in altitudinal and precipitation gradients and also certain degree of disturbance prevailing in this forest type.

Zone-1	Semi-Evergreen Forest	IVI	Moist Deciduous Forest	IVI	Dry Deciduous Forest	IVI	Degraded Forest	IVI
	Mangifera indica	40.15	Terminalia alata	39.99	Xylia xylocarpa	45.89	Cleistanthus collinus	53.14
	Garuga pinnata	15.98	Xylia xylocarpa	22.22	Anogeissus latifolia	24.48	Anogeissus latifolia	40.89
	Buchanania lanzan	15.86	Pterospermum xylocarpum	19.26	Terminalia alata	12.42	Xylia xylocarpa	36.66
	Xylia xylocarpa	15.39	Bursera serrata	9.15	Stereospermum suaveolens	11.71	Lannea coromandelica	17.00
	Stereospermum suaveolens	15.38	Cassia fistula	8.53	Lannea coromandelica	10.97	Terminalia alata	14.51
	Terminalia alata	15.18	Bombax ceiba	7.74	Grewia tilaefolia	9.96	Grewia tilaefolia	14.50
	Macaranga peltata	15.15	Terminalia bellirica	7.38	Tectona grandis	9.78	Garuga pinnata	11.98
	Memecylon edule	10.20	Anogeissus latifolia	7.36	Garuga pinnata	8.78	Stereospermum suaveolens	7.55
	Syzygium cumini	9.66	Syzygium cumini	6.81	Pterospermum xylocarpum	7.29	Dalbergia paniculata	7.29
Zone-2	Pterospermum xylocarpum	8.10	Lannea coromandelica	6.67	Lagerstroemia parviflora	6.75	Diospyros melanoxylon	6.44
			Moist Deciduous Forest	IVI	Dry Deciduous Forest	IVI	Degraded Forest	IVI
			Limonia acidissima	10.47	Chloroxylon swietenia	14.83	Cleistanthus collinus	23.55
			Cassia fistula	10.15	Anogeissus latifolia	9.50	Madhuca indica	7.52
			Terminalia alata	9.42	Cochlospermum religiosum	9.27	Mangifera indica	6.99
			Madhuca indica	7.28	Sterculia urens	8.15	Vitex peduncularis	6.94
			Sterculia urens	7.19	Tectona grandis	8.10	Butea monosperma	6.57
			Polyalthia cerasoides	6.98	Pterocarpus marsupium	7.55	Melia dubia	6.08
			Mangifera indica	6.71	Cassia fistula	7.42	Anogeissus latifolia	5.82
			Chloroxylon swietenia	6.60	Terminalia alata	7.09	Wrightia arborea	5.69
			Cochlospermum religiosum	6.40	Madhuca indica	6.80	Holoptelea integrifolia	5.49
			Mallotus philippensis	6.23	Boswellia serrata	5.96	Cassia fistula	5.48
			Red Sanders Mixed Forest	IVI	Hardwickia Mixed Forest	IVI	Southern Thorn Forest	IVI
			Pterocarpus santalinus	36.72	Hardwickia binata	41.50	Acacia chundra	30.67
			Albizia odoratissima	30.13	Anogeissus latifolia	17.24	Chloroxylon swietenia	21.32
			Anogeissus latifolia	12.87	Pterocarpus marsupium	8.15	Lannea coromandelica	10.75
			Hardwickia binata	9.08	Cochlospermum religiosum	8.08	Diospyros chloroxylon	9.26
			Terminalia alata	7.80	Terminalia alata	6.98	Acacia leucophloea	8.08
			Polyalthia cerasoides	6.22	Sterculia urens	6.76	Albizia amara	7.70
			Cassia fistula	5.99	Soymida febrifuga	6.19	Gyrocarpus americanus	7.04
			Cochlospermum religiosum	5.95	Bauhinia racemosa	5.10	Hardwickia binata	6.65
			Sterculia urens	5.90	Limonia acidissima	4.64	Bridelia montana	6.36
			Chloroxylon swietenia	5.67	Boswellia serrata	4.50	Atalantia monophylla	6.03

Table 4a. Important value index for the dominant tree species based on random for different vegetation types analyzed in Northern and Southern Eastern Ghats of Andhra Pradesh, India

Site 1		Site 2		Site 3	
Species	IVI	Species	IVI	Species	IVI
Xylia xylocarpa	72.46	Xylia xylocarpa	67.23	Schleichera oleosa	39.98
Dillenia pentagyna	20.97	Bursera serrata	26.43	Pterocarpus marsupium	26.05
Lagerstroemia parviflora	20.82	Terminalia alata	20.09	Bauhinia vahlii	22.52
Dendrocalamus strictus	18.04	Ougenia oojeinensis	18.04	Grewia tilaefolia	21.41
Anogeissus latifolia	17.98	Grewia tilaefolia	13.43	Mangifera indica	17.18
Buchanania lanzan	15.68	Pterocarpus marsupium	11.64	Mallotus philippensis	14.54
Cleistanthus collinus	12.81	Syzygium cumini	7.96	Gmelina arborea	13.53
Terminalia alata	12.39	Diospyros sylvatica	7.89	Cassia fistula	12.69
Terminalia bellirica	10.35	Semecarpus anacardium	7.04	Garuga pinnata	11.39
Pterocarpus marsupium	10.22	Bombax ceiba	6.47	Terminalia alata	9.43

Site 4		Site 5		Site 6	
Species	IVI	Species	IVI	Species	IVI
Chloroxylon swietenia	41.84	Pterocarpus marsupium	27.96	Terminalia pallida	35.19
Albizia amara	28.47	Lannea coromandelica	24.97	Pterocarpus santalinus	30.96
Diospyros chloroxylon	19.95	Anogeissus latifolia	20.86	Anogeissus latifolia	22.00
Ixora arborea	17.09	Dalbergia paniculata	20.39	Terminalia chebula	14.79
Premna tomentosa	16.65	Mitragyna parvifolia	13.72	Gardenia gummifera	14.45
Anogeissus latifolia	16.40	Grewia tilaefolia	12.01	Dolichandrone atrovirens	12.14
Acacia chundra	11.26	Lagerstroemia parviflora	10.98	Buchanania lanzan	10.15
Hildegardia populifolia	10.72	Bambusa arundinacea	10.81	Phyllanthus emblica	9.70
Commiphora caudata	9.59	Terminalia alata	10.68	Chloroxylon swietenia	9.04
Santalum album	9.52	Madhuca indica	8.46	Madhuca indica	8.88

Table 4b. Important value index for the dominant tree species based continuous plots in Northern and Southern Eastern Ghats of Andhra Pradesh, India

In the Southern Eastern Ghats (Zone-2) of Andhra Pradesh, we observed locale-specific formation, which is, characterized as Red-sander (*Pterocarpus santalinus*) mixed forest and Hardwickia (*Hardwickia binata*) mixed forest. Red-sander mixed forests are primarily deciduous system having *Pterocarpus santalinus* (36.72) as dominant species and secondary composition of *Anogeissus latifolia* (30.13), *Hardwickia binata* (9.08) and *Terminalia coriacea* (7.80). In Hardwickia mixed forest, *Hardwickia binata* (41.50) forms a community with *Anogeissus latifolia* (17.24), *Pterocarpus marsupium* (8.15) and *Cochlospermum religiosum* (8.08). These forests in both the zones are mainly dominated by *Cleistanthus collinus* species and also existences of some primary and secondary succession species.

For the transect of the 6 sites the dominance (IVI) varied a lot with very less species common in all the sites. Site 1 and 2 was predominated by *Xylia xylocarpa* (72.46 and 67.23 respectively), followed by *Dillenia pentagyna* (20.97), *Lagerstroemia parviflora* (20.82) and *Anogeissus latifolia* (17.9) in site 1 (Table 4b). In the case of site 3 the structure was predominantly of *Schleichera oleosa* (39.98), *Pterocarpus marsupium* (26.05), *Grewia tilaefolia* (21.41) and *Mangifera indica* (17.18). Contrastingly zone-2 was characterized by dry deciduous forest with *Chloroxylon sweitenia* (41.84), *Pterocarpus marsupium* (27.96) and *Terminalia pallida* (35.19) dominating site 4, 5 and 6 respectively.

3.1.3 Tree family dominance

For the random plots, a total of 95 families having 8,323 individuals were recorded from zone-1 and 17,383 individuals belonging to 124 families in zone-2. Taxonomically well-

represented families include Fabaceae (101), Euphorbiaceae (58), Rubiaceae (51) and Acanthaceae (48). Dominant families with respect to number of individuals are Euphorbiaceae (1786), Mimosaceae (1669), Combretaceae (1606), Fabaceae (1577), Rubiaceae (1368) and Caesalpinaceae (1282). Families with rare occurrences represented by single and double species were 66 for the whole study area.

For the continuous plot of the six sites, a total of 57 families belonging to 2,457 individuals were recorded from the present study. Taxonomically well-represented families include Rubiaceae (18), Euphorbiaceae (16), Fabaceae (11) and Caesalpiniaceae (9). Dominant families with respect to number of individuals are Mimosaceae (337), Combretaceae (274), Fabaceae (191), Rubiaceae (154) and Caesalpinaceae (138). Families with rare occurrences represented by single and double species were 36 for both the study sites. Top ten families explain the species characteristics and found to be 66% (1620 individuals out of 2,457 individuals) dominant for the study site.

3.1.4 Species accumulation curve

Species accumulation curve for the random plots showed different flattening levels in vegetation types of both the zones. The species accumulation as a function of number of individuals is given in Fig. 3a. Deciduous forest in both the zones showed a clear tendency towards flattening of the curve; however, zone-2 shows further increment due to its high species richness. Contrastingly, moist deciduous in both the zones doesn't show a typical flattening compared to the deciduous system. It seems that moist deciduous forest need to

Fig. 3a. Species accumulation vs. number of individuals in Southern and Northern zones of Eastern Ghats, Andhra Pradesh

Fig. 3b. Species accumulation curve for the six transects in Northern and Southern Eastern Ghats of Andhra Pradesh

be characterized and analysed based further on its altitudinal and climatic conditions to derive a species-area relation. The species-accumulation curves for the continuous plots of the six sites are given in Fig 3b. Site 1 and 4 were initially steep, and later we observed a tendency towards flattening and similar such pattern was observed for the Site 5 & 6. Site 2 & 3 didn't reach an asymptote due to high species richness and as well landscape heterogeneity.

3.1.5 Stand density and basal area

Stand density and basal area for the random plots in both the zones of deciduous forest is higher compared to other forest classes (Table 2). In zone-1 of deciduous forest stand density was much higher (486 stems ha⁻¹ and 19.04 m²ha⁻¹ basal area), when compared to zone-2 having 386 stems ha⁻¹ and 14.67 m²ha⁻¹ basal area. Moist deciduous forest of the zone-1 & 2 are in the range of 257-370 stems ha⁻¹. Similarly such patterns were also observed in dry evergreen forests (266-334 stems ha⁻¹). Degraded forest in zone-1 was relatively higher (449 stems ha⁻¹) due to the selective felling for its timber extraction when compared to zone-2. Thorn forest in both the zones is having least stand density class compared to other types. Stand density and basal area (BA) for the continuous plots in *site 1, 2 and 3* is higher compared to *site 4, 5 and 6* (Table 2). *Site 2* has high stand density of 1050 stems ha⁻¹ (BA 17.61 m²ha⁻¹) as compared to *site 3* having high basal area of 24.42 m²ha⁻¹ (990 stems ha⁻¹). Least basal area is seen in *site 4* (4.35 m²ha⁻¹) and least stand density in *site 5* (614 stems ha⁻¹). This is due to the dry deciduous forest in zone-2 having less density and less biomass. The girth class distribution pattern for all the sites except *site 3* and *5* is basically “L” shaped for

the total number of individuals (i.e. $G \geq 10\text{cm}$) (Fig. 4). We observed girth class of 10-30cm was having high number of individuals (39%). These species itself doesn't support larger biomass and density as a result there is very less representation in girth class above 200cm.

Fig. 4. Girth Class distribution for the six transects in Northern and Southern Eastern Ghats of Andhra Pradesh

3.1.6 Statistical analysis on Dis(Similarity measures)

In the following significance levels are represented with asterisks: * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$, not significant values simply sport no asterisks.

3.1.6.1 Species richness

Apparently species richness is only very slightly influenced by fragmentation and disturbance (Fig. 5). There is even less impact of the fragmentation and disturbance categories a plot falls in onto species richness when the zones are considered separately (Fig. 6). In the light of this finding it is interesting whether beta-diversity is in contrast to species richness - influenced by fragmentation and disturbance and whether this effect might be also only visible when all data are considered together.

3.1.6.2 Compositional similarity

Richness differs only slightly between the zones (Fig. 7) and although it is not apparent in the Fig. 7, the difference in mean is significant according to a regular t-Test applied to the data. However, a NMDS plot of the data suggests an apparent and direct relationship between zone membership and species composition (Fig. 8). The plots of zone-1 are clearly separated (along the NMDS axes 2) from the plots of zone-2. Fig. 8 also hints at the reasons for the faster decay of similarity in zone-1 (as seen in Fig. 9). The majority of the plots of zone-1 is closely clumped together which means that they are all relatively similar in their species composition. However, there is also some spread in direction of the NMDS-axes 2. In geographic terms a higher likelihood of two plots further apart is being more different than close plots results. The three other tested grouping variables (which have been found to

explain most of the explainable variation in species richness in multiple regressions with backward selection) do not show a clear pattern in the NMDS plots (Fig. 8).

The `mrpp()` function of package `vegan` (Oksanen *et al.*, 2007) for the R Statistics System has been implemented to evaluate whether the plots of the two zones can be attributed to different vegetation types. The two zones are clearly distinct in their vegetation composition: The observed delta is significantly lower (0.89) than the expected delta (0.93, as determined by permutation) although the difference is not very large. Furthermore $A = 0.036$. A is a chance-corrected estimate of the distances explained by group identity. It can be compared to a coefficient of determination of a linear model (R^2). Thus, it shows that the grouping into the two zones based on species composition is not very clear. With other words they are less distinct in species composition than the NMDS suggests (Fig. 8, upper left panel). Therefore another, more robust test has been employed as well. The function `anosim [vegan]` provides basically the same test but acts on ranks instead of the original data. It reports an R of -0.28^{***} : The similarity among plots of one zone is significantly higher than the similarity between plots of different zones.

Because the zones showed considerable grouping in the NMDS, further NMDS plots were drawn for each zone separately, to evaluate whether the species composition could than be more clearly attributed to the membership to categories of fragmentation, disturbance and richness. Fig. 10 shows that this is not the case. When the zones are considered separately no clear groupings according to the categories of the mentioned variables occur.

Fig. 5. Richness (species number inside plots) is significantly lower in highly fragmented plots. With disturbance there is no influence. The categorization is very coarse. Note, that there the numbers of plots involved in the categories differ considerably. Overall significance was tested with simple anova (for fragmentation: $F = 0.13^{**}$, for disturbance: $F = 0.83^{ns}$). Inference regarding the difference between the classes was obtained with pairwise t-Tests ($\alpha = 0.05$). Bonferroni correction was applied.

Fig. 6. The relation between richness (species number inside plots) and fragmentation/disturbance is much less clear when the zones are considered separately: Only fragmentation classes in zone 2 artly show a significance impact on species richness. Note, that here as well the numbers of plots involved in the categories differ considerably. Overall significance was tested with simple anova. Zone 1: fragmentation: $F = 1.25_{ns}$, disturbance: $F = 0.80_{ns}$; Zone 2: fragmentation: $F = 7.13^{***}$, disturbance: $F = 0.027_{ns}$. Inference regarding the difference between the classes was obtained with pairwise t-Tests ($\alpha = 0.01$) and Bonferroni correction was applied.

Fig. 7. Difference in richness between zones 1 and 2 (Inference obtained with t-Test)

3.1.6.3 Combined index of species richness, fragmentation, and disturbance

The 3d-plot of the factor variables fragmentation (x-axis), disturbance (y-axis) and the continuous variable richness (z-axis) shows that there is no clear relation between these three. It was also experimented with just putting the categories together (leads to 21 different possibilities). However, these categories explain nothing, because there is no explainable way in which they influence for instance the distance decay relations (see Fig. 11).

3.1.6.4 Distance decay of similarity

There is only relatively slow distance decay of similarity when all data is analyzed together for each zone. However, beta-diversity structure is different for the two zones (Fig. 9). In Zone-1 similarity decreases much faster ($-0.00022/\text{km}$) compared to zone-2 ($-0.000088/\text{km}$). This is more than one order of magnitude and is also reflected in the intercept. The linear regression line of the distance decay relationship intersects the y-axis at a similarity value (Sørensen) of 0.23 for zone-1, whereas the intercept is only 0.11 for zone-2. Not only the distance decay after linear regression but also the spline regression lines show considerable differences between zone-1 and 2. In zone-1 the rate of decay changes heavily and after a rapid decrease from 0 to 100 km distance, the similarity declines much slower. This holds also true when the subsets are further subsetted and e.g. different fragmentation classes are considered (Fig. 12).

Within the zones the slope of the distance decay relationship differs only slightly but significantly between different fragmentation categories (Fig. 12). Only the slopes of the linear regression lines describing the distance decay in the fragmentation classes 1 and 2 of zone-1 are not significantly different (Table 5). The smoothed regression lines cannot be tested in this way but from the illustrations (Fig. 12) it is apparent that there are important differences between the different fragmentation classes.

Fig. 8. NMDS based on all data, with different coloring regarding the membership of plots to subsets of data. The subsetting factor names each plot. Apparently the plots of the two zones show a clear difference regarding their vegetation composition compared to the plots of zone-1. Such a clear pattern rarely can be achieved. When the coloring is done for the categories of fragmentation, disturbance and richness, it is apparent that these do not impact species composition. NMDS statistic: stress = 36.10.

Fig. 9. Difference in richness between zones 1 and 2 (Inference obtained with t-Test)

Fragmentation Class			dsl	ρ
Zone	nbx	nby		
1	1	2	0.0000063	0.405
1	1	3	0.00012	0.001
1	2	3	0.00012	0.001
2	1	2	-0.000019	0.001
2	1	3	0.000027	0.001
2	2	3	0.000046	0.001

Table 5. Differences in slope of the distance decay relationship between subsets of the data. Each of the subsets comprises all plots that fall into the respective fragmentation class. The slopes differ significantly between fragmentation classes with the exception of the comparison between fragmentation classes 1 and 2 in zone 1. Abbreviations: nbx – one of the compared subsets, nby – the other of the compared subsets, dsl – difference in slope, calculated by $sl_{nbx} - sl_{nby}$, ρ – p value.

The picture does not change much when disturbance classes are considered instead (Table 6). In this case in zone-1 the slope of the linear regression line that describes the distance decay relationship in disturbance class 3 (high) very clearly is significantly steeper compared to the slopes for the classes 1 and 2. The latter two do not differ significantly from each other and the slope is even (very slightly) steeper for disturbance class 2. In zone-2 the slope of class 2 is much steeper than in the disturbance classes 1 and 3 of this zone. This is even apparent in Fig. 13 and as well reflected in the significance tests represented in Table 6.

Fig. 10. NMDS based on all data, with different coloring regarding the membership of plots to subsets of data. The subsetting factor names each plot. Apparently the plots of the two zones show a clear difference regarding their vegetation composition compared to the plots of zone-1. Such a clear pattern rarely can be achieved. When the coloring is done for the categories of fragmentation, disturbance and richness, it is apparent that these do not impact species composition. NMDS statistic: stress = 36.10.

Disturbance Class			dsl	ρ
Zone	nbx	nby		
1	1	2	-0.000018	0.236
1	1	3	0.000079	0.004
1	2	3	0.000096	0.007
2	1	2	0.000032	0.001
2	1	3	0.0000025	0.328
2	2	3	-0.000029	0.026

Table 6. Differences in slope of the distance decay relationship between subsets of the data. Each of the subsets comprises all plots that fall into the respective disturbance class. The slopes differ significantly between disturbance classes with the exception of the comparison between disturbance classes 1 and 2 in zone 1 and the comparison between classes 1 and 3 in zone 2. Abbreviations: nbx - one of the compared subsets, nby - the other of the compared subsets, dsl - difference in slope, calculated by $s_{lnbx} - s_{lnby}$, ρ - p-value.

Fig. 11. 3d-plot of disturbance (x-axis), fragmentation (y-axis), and richness (z-axis). The latter is a continuous variable whereas the other two are factor variables. There is no joint relation between these three

Fig. 12. Slopes of the distance decay relationship for subsets of the data. Each of the subsets comprises all comparisons between the plots of one zone and one fragmentation class therein. Besides the fact that similarity decreases much faster with distance in zone-1; there are apparent differences between fragmentation classes. The spline regression was obtained with a lowess smoothing algorithm as offered by the function `lowess()` with `f=0.2` of the R package `stats`.

Fig. 13. Slopes of the distance decay relationship for subsets of the data. Each of the subsets comprises all comparisons between the plots of one zone and one disturbance class therein. Besides the fact, that similarity decreases much faster with distance in zone-1; there are apparent differences between disturbance classes. The spline regression was obtained with a lowess smoothing algorithm as offered by the function `lowess()` with `f=0.2` of the R package `stats`.

3.1.6.5 The influence of slope and aspect on similarity and distance decay

Slope and aspect show no influence on species composition. The similarity in species composition has been regressed against the dissimilarity regarding slope and aspect. No correlation (Mantel) has been found neither for zone-1 ($r = -0.0068$) nor for zone-2 ($r = 0.01$). This holds even when we controlled for the influence of altitude on this relation (partial Mantel test). In the latter case Mantel correlation values amount to $r = -0.019$ (zone-1) and $r = 0.01341$ (zone-2) respectively.

3.1.6.6 Continuous plots for the six sites

The vegetation composition of the 6 sites show considerable differences. This is clearly apparent in the DCA drawn from the data in Fig. 14 (a & b). Because there are very few species shared between plots (see Fig. 15 for more detail regarding this issue) and because there are much more species than plots (when each of the 6 sites is considered as a single sample) the metaMDS algorithm very fast finds a stable solution. After 2 runs a very low stress value of 3.21 results (see also Figure 14a).

Fig. 14. a and b: Ordination plots of the 6-sites data. The six transects vary considerable in their species composition. Both methods come to comparable results. Sites 3 and 4 are highly dissimilar. Sites 2, 5, and 6 build something like a cluster (but is relatively vague), whereas Site 1 is far from 3 and 4 and closer to the other three but at the same time relatively distinct from all other Sites.

When the quadrats (that make up the sites) are considered separately, it is not possible to calculate a NMDS with the metaMDS algorithm because a majority of the compared quadrats have no species in common. Nevertheless, this means that overall beta-diversity in trees is very high. A solution can be achieved with the slightly less robust isoMDS[MASS] function. It accepts any distance matrix achieved in advance (rather than calculating a distance matrix during the process) and does not feature several random starts with different starting configurations but only a simple iteration algorithm. The result is displayed in Fig. 16. The sites are relatively clearly separated, which indicates that the similarity among quadrats of a site is much higher than similarity across sites. This can be tested with the mrpp() function of package vegan for R (see above). Applied to the data the function returns the following statistics: $A = 0.11^{***}$, $\text{delta_obs} = 0.83$, $\text{delta_exp} = 0.94$. This indicates that the groups are distinct in their species composition

Fig. 15. Pairwise comparison of shared, not shared, and unshared species for all possible pairs of sites from the 6-sites data. Explanation: shared species occur on both of the compared sites, not shared species occur on only one of the compared sites, unshared species do not occur on both the compared sites. Note, that the fraction of shared species is always relatively small

Fig. 16. NMDS plot of the 6-sites data. Colors represent the different sites as indicated in the legend. Sites are relatively clearly separated. Especially sites 3 and 4 show almost no species overlap. The sites of zone 2 (4, 5, and 6) clump much closer together (compared to the sites of zone 1 (1, 2, and 3)). Furthermore interesting is the very clear separation of some quadrats in sites 1 and 2 (on the right hand side of the figure) because it occurs within the sites. The stress value 49.16 is rather high which indicates a not so good final solution.

Fig. 17. Comparison of similarity between the 6 sites. The letters above the boxes connects sites not significantly different in mean similarity. Medians are often very low (sites 1, 3, 4) because a lot of quadrats inside do not share any species at all (so similarity is zero)

Also beta-diversity (expressed by compositional similarity) differs significantly between sites (Fig. 17). Only the sites 4 and 5 do not significantly differ in their similarity structure. However they have also been quite similar in species composition (as seen in the NMDS plot in Fig. 16) with site 5 being clearly positioned between site 3 and 4. All of the above can partly be grasped also from the species matrix, wherein - even without ordering - it is obvious that only few species occur on more than one or on even more sites.

A moderate percentage of quadrats (47%) are clustered into the “right” cluster when site membership is (very simplistically) compared to cluster membership. This was obtained by computing a simple Wards clustering with `hclust[stats]` followed by the application of `cutree[stats]` which simply cuts the resulting dendrogram tree to obtain group (or cluster-) memberships for all tested objects (the quadrats in our case) when the number of groups has been specified.

4. Discussion

4.1 Phytodiversity assessment

4.1.1 Random plots

An analysis of various quantitative inventories of woody species ≥ 10 cm dbh across the tropics reveals a wide variation in the figures, ranging from 20 species ha^{-1} in flooded Varzea forest of Rio Xingu, Brazil (Campbell *et al.*, 1992) to 300 species ha^{-1} in terra firma, Yanamono, Peru (Gentry, 1988). Within peninsular India, in various quantitative inventories of a comparable area for the same tree girth threshold, in tropical forest sites of the southern Western Ghats, species richness ranged from 30 species ha^{-1} in Nelliampathy (Chandrashekara & Ramakrishnan, 1994), to 57 species ha^{-1} in Mylodai, Courtallum reserve forest (Parthasarathy & Karthikeyan, 1997a), to 64 to 85 species ha^{-1} in Kalakad (Parthasarathy *et al.*, 1992) and 90 species on a 3ha scale in Kalakad-Mundanthurai Tiger reserve (Giriraj, 2006). Compared to various moist tropical forest sites in other parts of the world our present study showed comparable species richness and diversity.

The absolute stand density of both the zones across different vegetation communities are ranging from 156 to 486 trees ha^{-1} , with a whole study area average of 365 trees ha^{-1} . Deciduous forests of the zone-1 had higher stand density of 486 trees ha^{-1} compare to the zone-2 having 386 trees ha^{-1} , the reasons being favorable bioclimatic and edaphic conditions. These stand density are relatively lesser compared to the other sites in the Shervarayan and Kalrayan hills of Eastern Ghats, with the range of 640 to 986 trees ha^{-1} (Kadavul & Parthasarathy, 1999a) and 367 to 667 trees ha^{-1} (Kadavul & Parthasarathy, 1999b) respectively. Whereas the tree densities in various tropical evergreen forests of Western Ghats of peninsular India were: 574 to 915 stems ha^{-1} in medium elevation forest of Kalakad (Parthasarathy, 1999); 852 to 965 stems ha^{-1} in high elevation forest of Kalakad (Parthasarathy, 2001); 583 stems ha^{-1} in Kalakad-Mundanthurai area (Ganesh *et al.*, 1996); 482 stems ha^{-1} in Mylodai, Courtallam reserve forest (Parthasarathy & Karthikeyan, 1997a); a range of 270 to 673 trees ha^{-1} in the 30 ha of Varagalaia, Anamalais (Ayyappan & Parthasarathy, 1999), all these in southern Western Ghats and 635 stems ha^{-1} in Uppangala forest of central Western Ghats (Pascal & Pelissier, 1996). Density of trees (>30 cm gbh) in tropical forests ranges between 245 and 859 (Ashton, 1964; Campbell *et al.*, 1992; Richards, 1996) with intermediate values of 448 to 617 stems ha^{-1} in Costa Rica (Heaney & Proctor, 1990), 436 stems ha^{-1} in Reserva Forestal de San Ramon of Costa Rica (Wattenberg & Breckle,

1995), 420 to 777 stems ha^{-1} in Brazil (Campbell *et al.*, 1992) and 639 to 713 stems ha^{-1} in Central Amazonia (Ferreira & Prance, 1998).

The basal area for both the zones is ranging from 2.89 and 40.95 m^2ha^{-1} for ≥ 30 cm girth threshold. Thorn forest of the zone-1 had least basal area and high basal area was observed in the semi-evergreen forest of northern Eastern Ghats (40.95 m^2ha^{-1}). The mean basal area value of the present study is also lesser than the values for the comparable girth threshold of ≥ 30 cm gbh of several other tropical forests: 28.1 and 30.8 m^2ha^{-1} respectively of dry evergreen forest sites of Kuzhanthaikuppam and Thirumanikkuzhi (Parthasarathy & Karthikeyan, 1997b) Puthupet (Parthasarathy & Sethi, 1997) on the Coromandel coast of south India; 24.2 m^2ha^{-1} of Malaysia (Poore, 1968), 27.6 to 32.0 m^2ha^{-1} and 25.5 to 27.0 m^2ha^{-1} of Brazilian Amazon (Campbell *et al.*, 1986, 1992); 27.8 and 41.67 m^2ha^{-1} of Costa Rica (Lieberman & Lieberman, 1987; Watterberg & Breckle, 1995); 32.8 to 40.2 m^2ha^{-1} of Central Amazonian upland forest (Ferreira & Prance, 1998); 42.6 m^2ha^{-1} of Courtallam reserve forest in the Indian Western Ghats (Parthasarathy & Karthikeyan, 1997a); 39.7 m^2ha^{-1} of Uppangala forests, central Western Ghats, India (Pascal & Pelissier, 1996); and 25.91 to 47.75 m^2ha^{-1} in the 30 ha of Varagalaia, Anamalais, southern Western Ghats (Ayyappan & Parthasarathy, 1999). But a value of present study is lesser than: 53.3 to 94.6 m^2ha^{-1} and 55.3 to 78.3 m^2ha^{-1} of Kalakad, southern Western Ghats, India (Parthasarathy 1999; Parthasarathy, 2001) and the values of a couple of other tropical forests: 47 (for alluvium) to 49.5 m^2ha^{-1} (for slope forest) of New Caledonia (Jaffre & Veillon, 1990), and 62 m^2ha^{-1} of Monteverde, Costa Rica (Nadkarni *et al.*, 1995).

In both the zones, family-wise five predominant families explain the dominance of the forests which includes Combretaceae, Mimosaceae, Euphorbiaceae, Caesalpiniaceae and Rubiaceae. It contributes 39% of the family dominance which characterize the tree community pattern and in close range with other tropical forests regions (Gordon *et al.*, 2004; Linares-Palomino & Ponce-Alvarez, 2005) while the other Indian Eastern Ghats site, where the family Oleaceae (26.6%) dominated (Kadavul & Parthasarathy, 1999a) and in dry evergreen forests in south India, where the Melastomataceae and Rubiaceae with 56% dominated (Parthasarathy & Karthikeyan, 1997b).

The trend of decreasing diversity and density with increasing girth class is in conformity with the studies of Chittibabu & Parthasarathy (2000); Jeffre & Veillon (1990); Kadavul & Parthasarathy (1999a, b); Newbery *et al.*, (1992) and Pajmans (1970). Both the zones had typical reverse J-shaped structure for girth frequency (Fig. 4o). Northern region of the Andhra Pradesh explains mature stands in all the girth-class with good regeneration were in close conformity with other tropical forests around the world (Chittibabu & Parthasarathy, 2000; Kadavul & Parthasarathy, 1999a, b; Manokaran & Kochummen, 1987; Nadkarni *et al.*, 1995; Sukumar *et al.*, 1992).

4.1.2 Continuous plots for the six sites

A total of 197 species, 139 genera and 57 families (Table 3) were stated from six transects covering three-ha of the tropical forests in Northern and Southern Andhra Pradesh, Eastern Ghats. Species richness (43-72 species ha^{-1}) and species diversity 2.9-3.6 H' are comparable with the other sites in the Eastern Ghats. The mean value of 60 species ha^{-1} recorded in the present study is higher than that of 43 species ha^{-1} in Shervarayan hills (Kadavul & Parthasarathy, 1999a), 57 species ha^{-1} in Mylodai forest of Courtallum (Parthasarathy & Karthikeyan, 1997b). In Mudumalai tropical forest, Western Ghats, the 12 most common

species made up to 90.6% while 7 species were represented by only one individual (Sukumar *et al.*, 1992).

Species number per ha found in the present study is smaller in comparison with Malaysian lowland rain forests having 164 and 176 species (Malaysia, Wyatt-Smith, 1966), 150 species (Indonesia, Whitmore, 1990), 223 and 214 species ha⁻¹ (Malaysia, Proctor *et al.*, 1983). The wide range of species number 43-72 found in the present study plots can be attributed to the change in elevation, and bioclimatic variations. As compared to the tropics, neo-tropics show a much more complicated situation. In 1 ha plots of tropical rain forests, 91 species (Guiana, Davis & Richards, 1933), 87 species (Brazil, Black *et al.*, 1950) and 83 species (Venezuela, Jordan *et al.*, 1989) with DBH >10cm were reported. These values are lower than in the forest investigated in Xishuangbanna, SW China with 119 species (Cao & Zhang, 1997) and in present study (153 species). Such species diversity pattern may diminish as a function of altitude (Lieberman *et al.*, 1996).

The mean stand density of 409 stems ha⁻¹ and range of 307 to 525 stems ha⁻¹ in the tropical forests of northern Andhra Pradesh is well within the range of 276 - 905 stems ha⁻¹ reported for trees ≥10cm gbh in the tropics (Ghate *et al.*, 1998; Sundarapandian & Swamy, 1997; Sukumar *et al.*, 1997 & Murali *et al.*, 1996). This range of stand density in the present study is comparable with the other Eastern Ghats sites (Shervarayan hills - Kadavul & Parthasarathy, 1999a; Kalrayan hills - Kadavul & Parthasarathy, 1999b; Coromandel coast - Parthasarathy & Sethi, 1997). Low density was observed in other tropical sites across the world, which includes Costa Rica - 448 to 617 ha⁻¹ (Heaney & Proctor, 1990); Brazil - 420 to 777 ha⁻¹ (Campbell *et al.*, 1992); Malaysia - 250-500 ha⁻¹ (Primack & Hall, 1992).

The species-accumulation curve (Fig. 5) for the six different sites varied because of the changes in topography and rainfall. *Site 1* and *4* were initially steep, and later we observed a tendency towards flattening and similar such pattern was observed for the *Site 5* & *6*. *Site 2* & *3* didn't reach an asymptote due to high species richness and as well landscape heterogeneity. Similar patterns were noticed in different areas of Eastern and Western Ghats (Kadavul & Parthasarathy, 1999 a, b; Parthasarathy, 1999; Parthasarathy, 2001).

The most obvious variation in tree species and the proportion of dominant species in the six sites can directly be attributed to altitudinal and rainfall distribution. Particularly species richness increase at moderate elevation and beyond the altitude range, there is tendency towards decline (Giriraj *et al.*, 2003); similar pattern was observed in *site1*. Families with rare occurrences represented by single and double species were 36 for both the study sites.

Current study identified 57 families and the most predominant species rich families are Rubiaceae (18), Euphorbiaceae (16), Fabaceae (11) and Caesalpiniaceae (9) and similar such predominance were recorded from Shervarayan hills (Kadavul & Parathasarthy, 1999a). Steege *et al.*, (2000) and Martin & Aber (1997) reported Leguminosae as the most abundant family in neo-tropical forests. Top ten families explain the species characteristics and found to be 66% (1620 individuals out of 2,457 individuals) dominant for the study site.

Girth class frequency showed L-shaped population structure (Fig. 4) of trees except for *site 3* and *5*. This pattern is in conformity with many other forest stands in Eastern & Western Ghats such as Shervarayan hills (Kadavul & Parathasarthy, 1999a); Kalrayan hills (Kadavul & Parthasarathy, 1999b); Kakachi (Ganesh *et al.*, 1996); Uppangala (Pascal & Pelissier 1996); Mylodai-Courtallum RF (Parthasarathy & Karthikeyan, 1997b). *Site 3* & *5* didn't have a clear population structure might due to anthropogenic pressure in the form of shifting cultivation for their livelihood. In general the Northern Eastern Ghats (EG) of Andhra Pradesh (AP) exhibit large-scale deforestation as observed in Chapter-3 and southern EG of AP do have

pressure on the forests and these region having low altitudinal and precipitation formation resulted to low-level of population structure.

4.2 Spatial patterns of phytodiversity using Dis (Similarity measure)

Generally it is assumed that fragmentation and disturbance have a considerable influence on species richness (Connell, 1978; Huston, 1979). However, in the data set from the Eastern Ghats, this is only partly the case. Disturbance does not seem to drive species richness in the investigated area (Fig. 5 and 6). On the other hand this result might hint at a problem with the disturbance classification.

4.2.1 Compositional similarity

The separation of the plots in zone 1 from the plots of zone-2 is relatively clear (along the NMDS axes 2 in Fig. 8). Such obvious grouping is rarely found in ecological data sets. This means that the two zones are relatively distinct in their vegetation composition. However, astonishingly there is no further grouping within the zones regarding to the categorical parameters fragmentation, disturbance, and richness (also Fig. 8). When the zones are considered separately (Fig. 10) it becomes even more obvious that these parameters (at least in their representation of the actual research) do not drive the differentiation in species composition. Thus, not only richness but also species composition is not driven by disturbance or fragmentation.

Often richness drives compositional similarity of plots because plots with largely different species number very naturally tend to have only very few species in common. However, even that is not the case in the present data (Fig. 10). This holds also when the classification is much finer than displayed in Fig. 10. One reason for that might lay in the overall high beta-diversity in the region: The intercept of the distance decay relationship is comparably low (see e.g. Condit *et al.*, 2002 for comparison data from the Neotropics) which indicates a low similarity (and therewith high beta-diversity) even at short distances between plots.

Species richness, fragmentation and disturbance all have only very minor influence on species composition. Furthermore they are not linearly related to one another. Therefore a joint index cannot be build. If something like a surrogating indicator is the aim, the environmental parameters recorded have to be much more numerous. Furthermore, they should preferably be on continuous scales.

4.2.2 Distance decay

Similar findings are to be stated regarding the rate of the decrease of similarity with distance. Compared to data from the Neotropics (e.g. Condit *et al.*, 2002, 0.0019-0.00055/km) the distance decay rate in zone-1 (0.00022/km) fits nicely in. Astonishingly the rate is much lower in zone-2 (0.000088/km) and as already discussed in the previous paragraph, the intercept is also very low. This means that it doesn't matter how far two plots are from each other. There is always the chance that two plots can be very different regarding their tree species composition.

But even at this low decay rate a phenomenon occurs which seems to be ubiquitous to all distance decay data: There is comparably faster decrease on short distances. This has also been reported by (Jurasinski, 2007) who attributed it to the predominance of dispersal over niche assembly in the short range around vegetation samples. In the investigated data it can be found on all evaluated subsets of the data. This supports the idea of a ubiquitous pattern

in species assembly that bases on the predominance of neutral (Hubbell, 2005) versus niche assembly (Leibold, 1995) on different spatial scales.

The results of the distance decay evaluation indicate that the change of compositional similarity between plots with geographic distance follows different paces depending on fragmentation/disturbance. However the most impressive difference exists between the two zones. So the question arises, what is responsible for the differences in species similarity and distance decay relationship between the two zones? We have already learned above, that this cannot be directly attributed to differences in richness. And in the NMDS the grouping is not as clear with richness as the grouping variable compared to the zones (Fig. 8).

4.2.3 Slope and aspect

The variability of slope and aspect has no influence on species composition. This is in contradiction to findings from semi-arid vegetation (Badano *et al.*, 2005; Jurasinski, 2007; Sternberg & Shoshany, 2001). The difference in radiation which in e.g. Mediterranean ecosystems influences a lot of other factors (heat, moisture, evapotranspiration, etc.) is not an issue in tropical systems. Therefore slope and aspect cannot be used as explaining variables for the species composition of the plots. Thus similarity-distance function might predict the slope of a power-law species area curve (Condit *et al.*, 2002). Based on this characteristic the study concludes that it is an appropriate measure of beta-diversity. Already MacArthur (1965) proposed to use species-area curves as an analytical tool to diversity taking the intercept of the curve as a measure of 'alpha-diversity' and the slope parameter as a measure of 'beta-diversity' (see also Caswell & Cohen, 1993; Ricotta *et al.*, 2002). The present study stated that none of the recorded variables provides a good estimator for species richness or species composition. To evaluate the underlying factors many more and preferably continuous environmental variables should be recorded.

4.2.4 Continuous plots for the six sites

The 6 sites that have been investigated in detail regarding tree species composition can - with the help of ordination techniques be grouped. However, this grouping is not very meaningful because most of the sites cannot be grouped regarding their species composition. Only the *sites* 2, 5, and 6 have some more species in common which would allow the specification of a common vegetation type shared by these three sides.

It may be a problem of small sample size that the quadrats of *site* 5 are intermediate in their species composition between quadrats of *site* 3 and *site* 4 (Fig. 16). Otherwise it is astonishing that some of the quadrats in *site* 5 have a lot in common (species wise) with quadrats in *site* 3, which is in the other zone. This leads to the suggestion that the sample is too small for a classification of vegetation types: From the species matrix it is obvious that only few species occur on more than one or on even more quadrats.

The comparison between the wards clustering and the forced grouping into site membership reveals that there are quite some matches. However, this is relatively simplistic because it is not tested whether a quadrat is ordered together with quadrats of its site. This would be a better test, but this is not easily achieved because it is hard to define rules, which can be applied to such an evaluation. If 30 of the quadrats in on site are clustered into one cluster and 30 into other cluster - which is only a very simple case - the problems already start how to evaluate the assignment to several clusters. The simplistic measure already

shows that the differentiation in species composition is largely driven by the position in sites. However, on smaller scale vegetation types (or better groupings based on tree species data) might be identifiable.

5. Conclusion

The methodology developed for the comparison of multiple plots has been applied to a data set of vegetation in the Eastern Ghats of Andhra Pradesh to assess vegetation dis(similarity) and also evaluate transitional ecosystem. Whittaker's (1960) concept for assessing diversity has triggered a lot of development in ecology. However, especially the term 'beta-diversity' has begun to take on relatively different meanings and thus is a rather confusing concept. The terminological ambiguity is an obstacle to the development in all fields requiring more than inventory data ('alpha' or 'gamma-diversity' sensu Whittaker). Compositional (dis) similarity between samples ('differentiation diversity') and the variation of inventory diversity across scales ('proportional diversity') are important fields for future research, which should not be neglected due to unclear concepts.

Research and data recording in vegetation ecology should be spatially and temporally explicit. Even when no spatial analysis is intended, this might provide for the incorporation of data in later meta-analyses. Different sample designs needs (random, stratified and hexagonal grid) to be validated for different ecosystems prior applying this method, as it is efficient for long-term monitoring purpose. Furthermore it allows tracking temporal changes in spatial patterns through periodically repeated sampling. The changes in spatial patterns can be assessed statistically (Jurasinski & Beierkuhnlein, 2006) and suggested hexagonal grids are efficient method for the investigation and monitoring of spatio-temporal patterns on various scales.

6. References

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The Dynamical Processes of Biodiversity - Case Studies of Evolution and Spatial Distribution

Edited by PhD. Oscar Grillo

ISBN 978-953-307-772-7

Hard cover, 366 pages

Publisher InTech

Published online 02, December, 2011

Published in print edition December, 2011

Driven by the increasing necessity to define the biological diversity frame of widespread, endemic and threatened species, as well as by the stimulating chance to describe new species, the study of the evolutive and spatial dynamics is in constant execution. Systematic overviews, biogeographic and phylogenetic backgrounds, species composition and distribution in restricted areas are focal topics of the 15 interesting independent chapters collected in this book, chosen to offer to the reader an overall view of the present condition in which our planet is.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

S. Babar, A. Giriraj, C. S. Reddy, G. Jurasinski, A. Jentsch and S. Sudhakar (2011). Spatial Patterns of Phytodiversity - Assessing Vegetation Using (Dis) Similarity Measures, The Dynamical Processes of Biodiversity - Case Studies of Evolution and Spatial Distribution, PhD. Oscar Grillo (Ed.), ISBN: 978-953-307-772-7, InTech, Available from: <http://www.intechopen.com/books/the-dynamical-processes-of-biodiversity-case-studies-of-evolution-and-spatial-distribution/spatial-patterns-of-phytodiversity-assessing-vegetation-using-dis-similarity-measures>

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