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PROBABILITY MODELS TO STUDY THE SPATIAL PATTERN, ABUNDANCE AND DIVERSITY OF TREE SPECIES

D.M.Gowda [†] and Praveenkumar ^{*}

ABSTRACT

Ecological communities are composed of complex vegetation that differs from community to community and also within the community. The variability of tree species in the community in relation to their environments can be studied by using different statistical tools. The present study was conducted to describe and also to quantify the spatial pattern, abundance and diversity of tree species in the Western Ghats of Karnataka. The spatial pattern of tree species was studied by using Poisson and Negative binomial distributions. Results indicate that most of the selected tree species followed Negative binomial distribution having clumped pattern. The Species abundance distribution was studied by using log series and lognormal distributions in six different forest types (Evergreen, semi-evergreen, moist deciduous, dry deciduous, scrub and shola forest types). All six different forest types followed lognormal distribution where as evergreen and shola forest types followed log series distribution also. Diversity of the tree species in different forest types was quantified by different diversity indices; it was found that evergreen forest is most diverse.

Key words: Probability distributions, spatial pattern, abundance, diversity, indices, community, tree species.

1. INTRODUCTION

Natural communities are complex and mixture of several species. Plant species in the communities are patchy in nature. When the patchiness has a certain amount of predictability so that it can be described quantitatively called as spatial pattern. The spatial pattern of single species may be random, clumped and uniform patterns. Random pattern is defined as the individuals which occur independently each other. The clumped pattern is, the presence of one individual which increases the probability of finding another individual in its vicinity is also referred as aggregated pattern. The regular or uniform pattern is one where the individuals are over dispersed such that individual presence reduces the probability of finding another individual nearby (Dale 1998).

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Spatial pattern for some important tree species were detected through discrete probability distributions and the same was quantified by using measurement of aggregations (Pielou 1969, Skellam 1953, Ludwig and Reynolds 1988).

The most striking and consistent phenomenon observed in synecology is that community which include few species that are dominant and over shadow all other species in their mass and biological activities. Some species are intermediate, abundant and some are rare.

So the obvious topic of interest in the phytocoenosis is to study the distribution of number of individual per species (abundance) (Whittaker 1965). These can be explained through the probability distribution based on Poisson family.

Along with the method of explaining the species abundance through statistical distributions, the abundance of species in the communities can be quantified by traditional method of measuring the diversity through diversity indices.

Hence, the present investigation was undertaken to examine the spatial pattern of most abundant species in the community, abundance and also diversity of tree species in different forest types.

2. METHODOLOGY

2.1 Data structure

For the present study only tree data were collected across Belgum to Mysore covering nine districts under Western Ghats of Karnataka State based on observational approach where ecologist make measurement on community over a wide range of conditions imposed by nature rather than by experimenter. The data were classified according to different vegetation based on dominant phenological types such as evergreen, semi evergreen, moist deciduous, dry deciduous, scrub and shola forest types. Sampled data were comprising of 533 sampling units (SU) i.e., quadrats each of size 30X30 m based on site specific random sampling with 0.01 % intensity. Tree (>10 cm girth at breast height, GBH) data comprised of 29086 individuals represented from 685 species out of 533 quadrats forming contingency table of size 685X533.

2.2 Spatial Pattern Analysis (SPA)

The spatial pattern analysis was carried out to detect the pattern of eight important most abundant species in the Western Ghats of Karnataka. Species were selected based on their highest relative density as suggested by Oosting (1956), Swindel (1983) and Dale and Mc Issac (1989). The selected species are *Terminalia paniculata*, *Terminalia tomentosa*, *Tectona grandis*, *Olea dioica*, *Lagerstroemia microcarpa*, *Anogeissus latifolia*, *Aporosa lindleyana*, *Xylia xylocarpa*.

Three different statistical models are related with three types of spatial patterns based on their mean and variance relationship. Poisson distribution (PD) where $\sigma^2 = \mu$ for random pattern, Negative binomial distribution (NBD) when $\sigma^2 > \mu$ for clumped pattern and Binomial distribution when $\sigma^2 < \mu$ for uniform pattern. Occurrence of uniform distribution in complex communities is very rare. Spatial pattern analysis (SPA) of different forest tree species involved testing the distribution of number of individual per sampling unit is random; if it is not accepted then agreement with clumped pattern was tested through NBD (Ludwig and Reynolds 1988). The frequency distribution for SPA consist of number of sampling units (N) with 0,1,2,3..., individuals for 8 different species selected from 685x533 contingency table based on maximum relative abundance. Where relative abundance (A) is

$$A = \frac{\text{Number of individual of a species}}{\text{Total number of individual of all species}} * 100 \quad (\text{Oosting 1956})$$

is independent of the area sampled.

Random pattern for selected species were tested by fitting Poisson distribution under the assumptions that each natural sampling Unit (SU) has equal probability of hosting an individual, occurrence individual in SU is not influenced by other and average number of individual per SU ($\bar{x}$) remains constant for all the SUs.

The Poisson model for number of individual (X) is

$$P(X = x) = \frac{\lambda^x e^{-\lambda}}{x!} \quad ; x = 0, 1, 2, \dots,$$

fitted by using estimate of λ . Probabilities were obtained through the recurrence relation

$$P(X = r + 1) = \frac{\lambda}{(r + 1)} * P(X = r) \quad ; \quad r = 0, 1, 2, \dots, \quad \text{where} \quad P(X = 0) = e^{-\bar{x}}.$$

The goodness of fit was tested by using χ^2 test criteria with q-2 degrees of freedom (df) under the null hypothesis that number of individual of a species occurring in a random pattern. 'q' is number of frequency classes after necessary pooling (Sokal and Rolf 1981).

If the Poisson distribution is not a good fit then we can conclude that the spatial pattern is not random i.e., non random pattern exists for that species.

Negative binomial distribution which is Generalized* and compound** distribution was used to detect the non random pattern i.e., clumped pattern in different species (when $\sigma^2 > \mu$) after rejecting the Poisson model (Pielou 1969).

The Negative binomial model for number of individual (X) is given by

$$P(X = x) = \left[\frac{\mu}{\mu + k} \right]^x \left\{ \frac{(k + x - 1)!}{x!(k - 1)!} \right\} \left[1 + \frac{\mu}{k} \right]^{-k}$$

$$; x = 0, 1, 2, \dots, \mu \geq 0, k \geq 0, 0 < p < 1$$

$$\text{Where, } p = \frac{k}{\mu + k} \text{ and } q = \frac{\mu}{\mu + k},$$

μ , Mean number of individual per SU

k , a parameter characterize the degree of clumping

This model was fitted by using estimate of μ i.e., $\bar{x}$ and estimate of k by $\hat{k}$ which was obtained after stabilization of left hand side (LHS) and right hand side (RHS) of the following iterative equation

$$\log_{10} \left(\frac{N}{N_0} \right) = \log_{10} \left(1 + \frac{\bar{x}}{\hat{k}} \right)$$

Where, N =Total number of SU in the sample, N_0 is number of SU with '0' individual.

$\hat{k}$ is initial estimate of k obtained as

$$\hat{k} = \frac{\bar{x}^2}{s^2 - \bar{x}} \quad (1)$$

Where, s^2 is sample variance and $\bar{x}$ is sample mean. The equation (1) itself can be used instead of iteration as $\hat{k}$ when $\bar{x} > 4$ (Southwood 1978). If k tends towards zero then it indicates maximum clumping.

The probabilities were obtained by the recurrence relation

$$P(r) = \left[\frac{\bar{x}}{\bar{x} + \hat{k}} \right] \left[\frac{\hat{k} + r - 1}{r} \right] P(r - 1) \quad \text{where,} \quad P(0) = \left[1 + \frac{\bar{x}}{\hat{k}} \right]^{-\hat{k}}$$

* **Generalized:** Suppose number of cluster follows random pattern with Poisson model and number of individual per cluster assumed to follow logarithmic distribution then probability generating function of number of individual over the entire cluster gives probability term of NBD.

** **Compound:** If all the SUs are dissimilar having mean density λ , then λ itself becomes random variables, if it assumes to follow Pearson type III distribution the probability term lead to NBD

The goodness of fit of observed and expected frequencies were tested by using χ^2 test criteria at $q-k-1$ degrees of freedom (df) where q =No. of classes, k = No. of parameters estimated. If Negative Binomial Distribution (NBD) is not rejected one may conclude that the number of individual per sampling unit of a species have clumped pattern.

Hence it is necessary to measure the degree of clumping or aggregation. The degree of aggregation was measured by using two indices viz., Green's Index and negative binomial parameter k .

Green Index was proposed by Green (1966) is independent of number of individuals in the sample and it is given as

$$GI = \frac{(s^2/\bar{x}) - 1}{n - 1}$$

it ranges from zero to one. If GI is towards zero then individuals of a species exhibits random pattern and a species exhibits clumping pattern when value of GI is towards one and if $GI = \{-1/(n-1)\}$ indicates maximum uniformity. (Elliot 1973a).

The NBD parameter ' k ' can also be used as a measurement of aggregation which is independent of random change in population size. Higher the value of k indicates lowers the degree of clumping and as value of k tends towards zero the clumping will be maximal.

2.3 Species abundance distribution

The species abundance distribution can be studied by resource apportioning models and statistical models. Resource apportioning models assumed that different species divide available resources equally. Where as statistical models have assumptions about the probability distribution. In present study two statistical models which are based on Poison

family of distributions viz., logarithmic distributions and log normal distributions were used to study the species abundance distribution for six different forest types.

The probability terms were obtained by compound Poisson probability function as

$$P_r = \int_0^{\infty} \left(\lambda^r e^{-\lambda} / r! \right) f(\lambda) d\lambda \quad ; \quad r = 0, 1, 2, \dots,$$

by substituting different density functions of $f(\lambda)$ (Pielou 1969).

Logarithmic distribution was fitted to the observed frequency distribution comprising n_1 number of species represented by one member, n_2 number of species represented by two member and so on having probability mass function, number of species represented by r individuals as

$$f_r = \frac{\alpha X^r}{r} \quad ; \quad r = 0, 1, 2, \dots, \quad \text{and } \alpha > 0 \text{ \& } 0 < X < 1 \quad (2)$$

The parameters α and X were estimated by solving equations $s = -\alpha \ln(1-X)$ and $\frac{\alpha X}{n} = 1 - X$ where s , is the number of species in the sample and n , is the total number of individuals in the sample and expected frequencies were obtained directly by the equation (2) on substituting the estimates of the distribution.

Since $\alpha = s\gamma$ and γ is expressed in terms of X as $\gamma = \frac{1}{-\ln(1-X)}$ as given by Pielou (1975) this distribution has only one parameter. Hence the goodness of fit of logarithmic distribution was tested by using χ^2 with $q-k-1$ df. If the test is non significant then that forest type can be explained through the logarithmic series model and $\hat{\alpha}$, an estimate of the parameter α can be used as index of diversity.

Lognormal distribution was fitted to study the species abundance distribution through Preston's (1948) octaves (midpoint of each group is double that of preceding group) method where no explicit expression is present for integral of probability term obtained through compound Poisson family distribution.

The lognormal distribution is given as $S(R) = S_0 e^{-(a^2 R^2)}$ where, $S(R)$ is number of species in the R^{th} octave from the modal octave, S_0 , is an estimate of the number of species in modal octave i.e., octave with more number of species and a , is an inverse measure of width of the distribution i.e., $a = \sigma/2$, (where σ is standard deviation).

The observed data according to Preston's method for fitting log normal distribution

were arranged in the form, $R_i = \log_2 \left(\frac{S_i}{S_0} \right)$, where S_i , is species abundance in i^{th} octave and S_0 , is species abundance in the modal octave. The parameter 'a' and S_0 were estimated to fit the distribution. Estimator for 'a' and S_0 are $\hat{a} = \sqrt{\frac{\ln[S(0)/S(R_{\max})]}{R_{\max}^2}}$ and $\hat{S}_0 = e^{(\ln S(R) + \hat{a}^2 \bar{R}^2)}$ where, $S(R_{\max})$ is observed number of species in the octave most distant from the modal. $R_{\max}$, Octave most distant from the modal octave, $\overline{\ln S(R)}$ is mean of logarithm of observed number of species per octave and $\bar{R}^2$ is mean of R_i^2 's.

There are two estimates of S_0 one based on above equation and other is number of species in the modal octave directly obtained through the frequency distribution itself.

Two expected frequencies obtained by two different set of estimators were tested by using χ^2 with q-k-1 df, where 'q' is number of octave classes and k is the number of parameters estimated. If any forest types fits well then that forest types is modeled as the log normal distribution then total number of species in for that particular forest types S^* , can be estimated by $\hat{S}^* = 1.77 * (\hat{S}_0 / \hat{a})$ using set of estimates $\hat{a}$ and $\hat{S}_0$ which yields lesser value in Chi-square test, so that one can obtain an estimate of number of unobserved species by the sample for different forest types.

2.4 Indices of diversity

Alfa (within habitat) diversity can be quantified through diversity indices apart from explaining them by statistical distribution. The diversity of the forest types have two components viz., weighted measure of s, number of species in the sample and the distribution of species abundance by evenness or equitability.

A collection is said to have high diversity if it has many species with their abundance distributed evenly. Conversely diversity is low when the species are few and abundance is uneven. Indices used to measure the diversity are viz., Simpson index and Shannon's index and Hill's numbers.

Simpson index:

Simpson (1949) proposed an index to measure the species diversity in a community and it is given as $\lambda = \sum_{i=1}^s p_i^2$ which ranges from 0 to 1, gives probability that two individual drawn at random from the population will belong to same species.

Where p_i : Proportional abundance of i^{th} species, $p_i = (n_i/n)$, $i=1, 2, \dots, s$.

n_i : Number of individual of i^{th} species and

n : Total number of individuals for s species in population.

The unbiased estimator of Simpson's index λ is

$$\hat{\lambda} = \sum_{i=1}^s \frac{n_i(n_i-1)}{n(n-1)}$$

If $\hat{\lambda}$ is towards zero indicates highest diversity and vice versa.

Shannon's index:

Shannon index to measure the species diversity in a community is

$$H' = - \sum_{i=1}^{s^*} p_i \ln p_i$$

where S^* , is number of species with known proportion abundance, $p_1, p_2, \dots, p_{s^*}$. in the community, S^* and p_i 's are population parameters, provides average uncertainty in predicting to which species an chosen individual at random from collection of 's' species will belong. Average uncertainty increases as number of species increases and distribution

becomes even. This index can be estimated as

$$\hat{H}' = - \sum_{i=1}^s \left[\left(\frac{n_i}{n} \right) \ln \left(\frac{n_i}{n} \right) \right]$$

Where n_i : number of individual belongs to i^{th} species in the sample.

n : Total number of individual in sample.

Hills numbers:

Index of diversity computed by Hill (1973) are easy to represented by general formula as,

$$N_A = \sum_{i=1}^s (p_i)^{\frac{1}{(1-A)}}$$

where p_i : is proportion of individuals belonging to i^{th} species.

$A=0,1,2$ orders are computed by measures of diversity

$N_0=s$, where s is total number of species in the sample,

$N_1=e^{H'}$, gives number of abundant species where H' is Shannon

index

$N_2=1/\lambda$, yields number of very abundant species.

As the species diversity also based on evenness, indices such as E_4 and E_5 are obtained by Hills numbers N_2 and N_1 .

$$E_4 = \frac{1/\lambda}{e^{H'}} = \frac{N_2}{N_1} \quad \text{and} \quad E_5 = \frac{(1/\lambda)-1}{e^{H'}-1} = \frac{N_2-1}{N_1-1}$$

E_4 tends towards one and E_5 towards zero as N_2 tends to N_1 , indicates not all but some species becomes more and more dominant in the community indicates diversity of that forest type is lesser. Hence along with the Hills diversity numbers and evenness indices one can easily interpret about the diversity of the particular forest type.

3. RESULTS AND DISCUSSION

Selected species were tested for their pattern by distribution method (Ludwig and Reynolds 1988). Initially existence of random pattern was tested by using PD for all 8 species independently as evoked by Blackman (1935), Greig and Smith (1952) and Kent and dress (1979). The results of all 8 species rejected the null hypothesis of PD indicated that non randomness pattern exist in these species. This was mainly because of reason that the variance was higher than that of mean number of individual per sampling unit. This non random pattern was then tested by applying generalized and compound NBD (Robinson1954) as suggested by Cole (1946) Archibald (1948), Bliss and Fisher (1953) and Hubbell (1979). Among eight selected species seven species agreed with NBD and hence it can be inferred that they exhibited the clumped pattern. The species *Tectona grandis* was not agreed with both random and clumped pattern.

After detection of the pattern it was quantified by using Green's index (GI) and NB parameter 'k'. The species *Terminalia paniculata* exhibited lowest degree of clumping with least value for GI (0.0059) and highest for 'k' (0.225). Where as species *Xylia xylocarpa* exhibited highest degree of clumping with higher value for GI (0.0194) and lowest value for 'k' (0.062). The results are given in Table (1).

The possible reason for this type of pattern exhibited by different species may be due to morphological, heterogeneous environmental, phytosociological and biological factors as suggested by Lamont and Fox (1978), (Dale 1998) and Campos *et al.*, (2000). This pattern may also be affected by the block size or quadart size which can be further explored by taking studies with different block sizes. These results are in conformity

with the results obtained by Blackman (1935), Fracker and Brischle (1944), Whitford (1949) and Ashby (1952), but contradicts the results of Wu Chang Zhen *et al.* (1979), Greig and Smith (1952a).

Log series and log normal distributions were used to study abundance distribution of tree species in different forest types. All six different forest types followed lognormal model, whereas the shola and evergreen forest types also agreed with log series distribution besides lognormal distribution. The 'good fit' with the log normal distribution for different forest types were in conformity with the results of Bulmer (1974), Kempton and Taylor (1978), Lamont and Fox (1978), May (1975), May (1981) and Sugihara (1980) and contrasts the results of Williams (1964), Holgate (1969) and Lamont *et al.*, (1977).

Estimation of total number of species S^* for all and hence number of unobserved species were computed as all the forest types as they followed lognormal distribution. Semi evergreen forest type exhibited highest number of unobserved species (173) in the sample. Since evergreen and shola forest type fitted well for log series distribution $\hat{c}$, estimate of the parameter in the distribution used as index of diversity. It was found that evergreen forest type exhibited maximum diversity which comprised value of 89.6 with long tail.

Result of diversity indices indicated that evergreen forest types exhibited maximum diversity among all forest types having maximum number of abundant species (131) and very abundant species (67) out of 414 species as computed by Hills numbers N_1 and N_2 along with lowest value exhibited by Simpson's index (0.015) and highest value for Shannon's index (4.87) having moderate evenness (0.51). Conversely, Dry deciduous forest types exhibited lowest diversity having lesser number of very abundant (14) species out of 205 species in that forest type having higher value (0.074) for Simpson's index and lower value for Shannon's index (0.39) with lesser evenness (0.39). Since Hills numbers are expressed in terms of abundant and very abundant species these are easy for interpretation as compared to Simpson's index and Shannon's index. The results of species abundance and diversity indices are presented in table 2.

4. SUMMARY

Ecological communities are composed of complex and mixture of several vegetation types which differ from the community to community and within the community. Ecological scientists have attempted to study this type of variability in the Western Ghats of Karnataka by several traditional methods. The present study was undertaken to investigate same by using different statistical distribution models.

Spatial pattern of most of the species have agreed with NBD having clumped pattern with variance greater than mean. NBD can directly used to detect the spatial pattern of the species when variance is higher than the mean. If NBD fits well then parameter 'k' of the distribution can be used to measure the degree of aggregation along with Green's index.

All six dominant phonological forest types followed lognormal distribution with respect to species abundance distribution. Hence log normal distribution model has been suggested to study the abundance distribution in the natural communities as compared to log series distribution. Lognormal distribution also provides an estimate of total number of species in that forest type.

Hills diversity numbers are suggested to measure the diversity of tree species which are easy for interpretation for different forest types which gives diversity directly in terms of number of abundant and very abundant species. Where as Simpson index, Shannon's index and $\hat{C}$ parameter of log series are in terms of probability and average uncertainty they are complex for interpretation about the species diversity compared to Hills numbers.

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Table1. Spatial pattern of 8 most abundant species with summary statistics

Species	n	M	Mean	Variance	PD	NBD	GI	'k'	Remarks on pattern
<i>Terminalia paniculata</i>	1398	232	2.62	24.14	**	ns	0.0059	0.225	Clumped
<i>Terminalia tomentosa</i>	1379	203	2.59	33.33	**	ns	0.0086	0.173	Clumped
<i>Tectona grandis</i>	896	119	1.68	16.43	**	**	0.0098	-	Neither Clumped nor random
<i>Olea dioica</i>	910	182	1.707	17.07	**	ns	0.0099	0.176	Clumped
<i>Lagerstroemia microcarpa</i>	673	178	1.26	11.98	**	ns	0.0126	0.207	Clumped
<i>Anogeissus latifolia</i>	1439	127	2.69	53.83	**	ns	0.0132	0.075	Clumped
<i>Aporosa lindleyana</i>	824	133	1.54	20.91	**	ns	0.0152	0.103	Clumped
<i>Xylia xylocarpa</i>	812	98	1.52	25.60	**	ns	0.0194	0.062	Clumped

*: Significant at 5% level

**: Significant at 1% level

ns: Non Significant

PD: Poisson distribution

GI: Green's Index

k: Negative binomial distribution parameter

m: Number of Quadrats in which species occurred

n: number of individual of a species

NBD: Negative Binomial distribution

Table2. Species abundance & diversity of different forest types with summary statistics.

Forest type	No. of SUs	S=N ₀	Log series	Log Normal	$\hat{C}$	$\hat{S}^{\dagger}$	$s-\hat{S}^{\dagger}$	Hill's numbers		Diversity indices		Evenness indices	
								N ₁	N ₂	$\hat{\lambda}$	$\hat{H}'$	E ₄	E ₅
Evergreen	158	414	ns	ns	89.6	522	108	131	67	0.015	4.87	0.51	0.51
Semi Evergreen	97	350	**	ns	-	523	173	99	47	0.021	4.60	0.48	0.42
Shola	12	130	ns	ns	50.1	172	42	66	39	0.025	4.19	0.59	0.59
Moist Deciduous	152	328	**	ns	-	481	153	71	30	0.033	4.27	0.43	0.42
Scrub	15	124	*	ns	-	213	89	43	18	0.055	3.75	0.43	0.41
Dry Deciduous	99	205	**	ns	-	337	132	35	14	0.074	3.56	0.39	0.37

$\hat{S}^{\dagger}$: Total number of species estimated by the estimates which yielded lower Chi-square in fitting of lognormal distribution.

$\hat{C}$: Index of diversity an estimate of parameter α of log series distribution

N₁ : Number of abundant species

N₂ : Number of very abundant species

s=N₀ : Number of species observed in the sample

(s- $\hat{S}^{\dagger}$): Total number of unobserved species

$\hat{\lambda}$: Simpson index $\hat{H}'$: Shannon's index