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# Neutral Theory and Species Abundance Distribution in Sinharaja Tropical Forest

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## 1 INTRODUCTION

Species abundance distribution (SAD) is the second most important macro-ecological pattern in tropical forests. In general, rank SAD shows positive skewed distributions due to the many singleton species found in tropical forests. Fisher log series and Preston octave curves (log normal distribution) were used to explain the SAD. Although Fishers log series can explain the long tail of SAD, it needs biological explanation. In contrast, Preston assumes that long tail of the SAD is a sampling effect and for large samples long tail of SAD distribution is diminished. Hubbell's neutral theory (Hubbell, 2001); a dispersal assembly theorem, considers species are functionally equivalent. This theory underlines that community is saturated and replacement is only possible when a tree dies. Species are functionally equivalent and all the off-springs have an equal chance possible of being replaced. According to Hubbell (2001), local community undergoes an ecological-drift over time. Extinction of rare species lead to mono-dominance in local community. However, this mono-dominance is delayed by the immigration ( $m$ ) of new species to the local community from the meta-community (Rosindell *et al.*, 2011).

Species abundance of a meta-community stays at the equilibrium between extinction and speciation rate ( $\nu$ ). Hubbell (2001) states that fundamental biodiversity number ( $\theta = 2J_M\nu$ ) and dispersal limitation ( $m$ ) alone can explain SAD of a local community. When  $m=0$  local community is fully isolated. When  $m=1$  local community is a nested subset of the meta-community. If neutral theory is true, then rank relative SAD under the neutral model should closely follow the empirical SAD of the community. This indicates that the species interaction has little effect on the shape of the SAD and the high species richness in tropical forests diminishes species interactions (Hubbell, 2006). Further, this will be useful for constructing SAD under neutral model for the considered forest plots. The main objective of this study is to find the best  $\theta$  and  $m$  values and explain the rank SAD using Hubbell's neutral theory.

## 2 METHODOLOGY

### 2.1 Study area

Sinharaja forest is a 500 m x 500 m (25-ha) plot which is located in the southwest



region of Sri Lanka. It is the largest block of relatively undisturbed lowland evergreen rainforest in Sri Lanka. The elevation range of Sinharaja FDP lies between 424 m and 575 m above sea level. Sinharaja is an UNESCO World Heritage Site at the center of the ever-wet southwestern region of Sri Lanka. It was established in 1993 by the University of Peradeniya and the Forest Department of Sri Lanka. The trees in the plot were censused from 1994 to 1996, where the diameters at breast height (dbh) of all freestanding stems greater than or equal 1 cm were measured. In Sinharaja 18,065 adults were found (trees with diameter of breast height  $\geq 10$ cm), belonging to 188 species. (Census year-1996)

## 2.2 Data set

Data from Sinharaja FDP which was initiated in 1996 was used to construct the empirical SAD. The data set contains 20 variables but only few of them are considered to this study (species name-sp and diameter of breast height-dbh). Hubbell (2001) assumes that the neutral theory works for the adult trees. In his seminal work he used trees with diameter

at breast height (dbh)  $\geq 10$ cm as adult trees. Therefore, in our study we considered only about adult trees (dbh  $\geq 10$ cm) in the 500x500 Sinharaja FDP. The  $\theta$  and  $m$  values for nine other forest plots were calculated using freely available data from the Centre for Tropical Forest Science/ Smithsonian Institution Global Earth Observatory network (<http://www.sigeo.si.edu/>). Each data set contains two sets of data for diameter of breast height (dbh)  $\geq 1$  cm and dbh  $\geq 10$ cm. For this study, only the trees with dbh  $\geq 10$  cm were considered from the latest census of each FDP.

## 2.3 Species abundance distribution

We first simulated local communities with different  $\theta$  and  $m$  combinations with fixed local community size ( $J=18,065$ ). Here,  $J$  is equal to the number of adult trees in the fully mapped forest plot (Sinharaja / Sri Lanka). A species generator (Etienne et al., 2005) was used to generate the species abundances for a local community with different  $\theta$  and  $m$  combinations (Table 1). In total there were 144  $\theta$  and  $m$  combinations.

**Table 1:**  $\theta$  and  $m$  combinations for fixed community size ( $J$ )

|          |      |     |      |      |      |      |     |     |     |     |     |    |
|----------|------|-----|------|------|------|------|-----|-----|-----|-----|-----|----|
| $\theta$ | 20   | 25  | 30   | 35   | 36   | 37   | 38  | 39  | 40  | 41  | 42  | 45 |
| $m$      | 0.01 | 0.1 | 0.13 | 0.14 | 0.15 | 0.16 | 0.2 | 0.3 | 0.5 | 0.8 | 0.9 | 1  |

Next best  $\theta$  and  $m$  combination was selected by minimizing the sum of squared difference of species rank relative abundance of neutral model and species

rank relative abundance of Sinharaja forest plot. Further we used likelihood maximization to estimate the two parameters  $\theta$  and  $m$  (Etienne *et al.*, 2005).

$$P[D | \theta, m, J] = \frac{J!}{\prod_{i=1}^s n_i \prod_{j=1}^J \Phi_j!} \frac{\theta^s}{(I)_J} \sum_{A=S}^J K(D, A) \frac{I^A}{(\theta)^A}$$

Where,  $\theta$  - Fundamental biodiversity number,  $m$  - Immigration rate,  $J$  - Total number of individuals,  $D$  - Abundance

distribution,  $s$  - Number of species,  $n_i$  - Number of individuals for the  $i^{\text{th}}$  species,  $a_i$  -  $i^{\text{th}}$  ancestor when it is the  $i^{\text{th}}$  species,  $A$ -

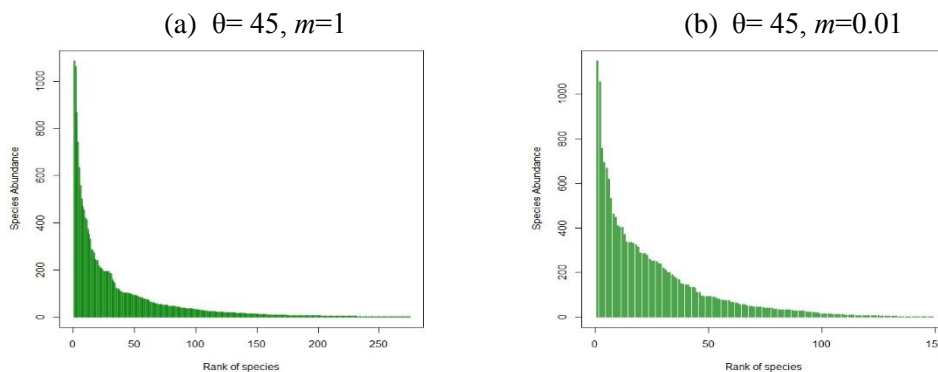


Summation of all the ancestors from the first species to the  $s^{\text{th}}$  species,  $I = m(J-1)/(1-m)$

Finally results from minimizing the sum of squared difference method and likelihood maximization method were compared. The statistical analysis was carried out using *R* software (*R* Core Team, 2014).

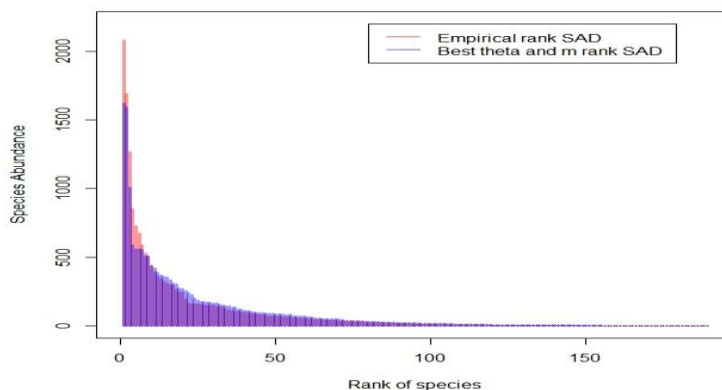
### 3 RESULTS AND DISCUSSION

When  $m$  is large we found out SAD of the local community is approximated to SAD of the meta-community. We also observed a long tail of rare species in SAD of the local community (Fig. 1a.). In contrast, when  $m$  is small, species richness is low and local community is isolated (Fig. 1b).



**Figure 1(a), (b):** Rank SAD for two different  $\theta$  and  $m$  combinations for a fixed local community ( $J=18,065$ ; equal to all the adult trees,  $\text{dbh} \geq 10$  cm, in the Sinharaja forest plot).

When,  $\{\theta = 40, m = 0.13\}$  rank relative SAD of the neutral community fitted to the empirical SAD. These are biologically acceptable (Figure 2).



**Figure 2:** Blue bars-Rank SAD for best  $\theta$  and  $m$  combinations ( $\theta = 40, m=0.13$ ) for a fixed local community size ( $J=18,065$ ; equal to all the adult trees in the Sinharaja forest plot). Red bars-Empirical rank SAD for all the adult trees in the Sinharaja forest plot. Purple bars-Overlapped empirical and best  $\theta$  and  $m$  rank SAD.

Etienne et al., (2005) suggested the maximum likelihood estimator method to find the best  $\theta$  and  $m$  combination. We

used his method to estimate the two parameters. But his method works partially. For Sinharaja, Lenda, and Edoro



forest plots give very large  $m$  values ( $m$  values which are nearly equal to one indicates no dispersal limitation and local community is a nested subset of meta-community). Such  $m$  values are biologically unacceptable. On the other

hand Etienne et al., (2005) gives low  $m$  values for Pasoh forest plot compared to BCI forest. However Hubell et al., (1997) found that species in Pasoh forest show high dispersal ability than the BCI forest.

**Table 2:**  $\theta$  and  $m$  combination for 10 forest dynamic plots in Centre for Tropical Forest Science (CTFS).

| Study plot     | Study area (ha) | Community size (yr.) (J) | Species Richness (S) | $\Theta$ | $m$   |
|----------------|-----------------|--------------------------|----------------------|----------|-------|
| BCI            | 50              | 20848 (2005)             | 227                  | 46.45    | 0.12  |
| EDORO          | 10×2            | 9382 (2000)              | 207                  | 36.06    | 0.999 |
| FUSHAN         | 25              | 19270 (2002)             | 77                   | 10.86    | 0.441 |
| KORUP          | 50              | 24591 (1998)             | 308                  | 52.73    | 0.547 |
| LAPLANADA      | 25              | 15013 (2003)             | 173                  | 30.1     | 0.405 |
| LENDA          | 10×2            | 7300 (2000)              | 213                  | 40.96    | 0.999 |
| MUDUMALAI      | 50              | 12579 (2000)             | 61                   | 8.3      | 0.925 |
| PASOH          | 50              | 28279 (2000)             | 671                  | 192.64   | 0.077 |
| SINHARAJA (SL) | 25              | 18065 (2001)             | 188                  | 29.15    | 0.999 |
| YASUNI         | 50              | 17434 (2003)             | 819                  | 205.97   | 0.406 |

## 4 CONCLUSIONS

In this study we found that when  $\theta=40$  and  $m=0.13$ , the empirical rank SAD of the neutral community is approximated to the rank SAD of the 25-ha Sinharaja forest plot. These results indicate species abundance distribution in the Sinharaja forest is largely driven by neutral process. When  $m$  is large we found out SAD of the local community is approximated to SAD of the meta-community. We observed a long tail of rare species in SAD of the local community in Sinharaja forest. Also when  $m$  is small, species richness is low and local community is isolated. We found that maximum likelihood estimation perform poorly for parameter estimation.

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