OPENING MINDS: RESEARCH FOR SUSTAINABLE DEVELOPMENT

Neutral Theory and Species-Area Relationship in Tropical Forests

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1 INTRODUCTION

The neutral theory of biodiversity provides a powerful framework for modelling macro-ecological patterns such as species-area-relationships (SAR) (Hubbell, 2006; Hubbell, 2001; Hubbell, *et al.* 1997). Species-area curves explain the relationship between area sampled and the number of species found. The classical niche theory (Hutchinson, 1957) and Hubbell's unified neutral theory are two well-known theories that can be used to explain the SAR. According to the niche theory species differences are important to explain the SAR. Therefore, niche theory expects that the shape of the species area curve to depend on the spatial arrangement of species, habitat fragmentation, and species interactions. In contrast, the neutral theory assumes all species in a community have the same competitive ability and have identical birth, death, growth and speciation rates. Therefore, it assumes that the species differences are irrelevant to explain the SAR. This theory emphasizes "zero-sum ecological drift" and dispersal limitation (*m*) alone can explain the species richness of a local community (Hubbell, 2001). Hubbell assumes a fundamental biodiversity number ($\theta = 2J_M \upsilon$) controls the meta-community species richness at an equilibrium between speciation (υ) and extinction. Further, Hubbell (2006) assumes that species interactions are weak in species rich forests (called species dilution effect). In tropical forests, species are well mixed and neighbourhood diversities are inconsistent (Hubbell, 2006). If the neutral theory is true, SAR under the neutral model should closely follow the empirical SAR. Deviations are expected when processes such as habitat association, dispersal limitation and species interactions are important for the spatial arrangement of the species. This study compares the shape of the empirical SAR of the 25-ha, fully mapped Sinharaja Forest Dynamics Plot (FDP) in Sri Lanka (Gunatilleke, *et al.* 2006) with the SAR under fully neutral model which has only two parameters, θ (biodiversity number) and m (dispersal limitation which indicate the probability of immigration) that coupled local community and meta-community. Additionally, we calculated the θ and m values for nine other forest plots (25-50ha) in different countries. This will be useful for constructing the SAR under neutral model for the considered forest plots. (Summarized details about these plots are included in Table 1)

2 METHODOLOGY

2.1 Study area

The area studied is the Sinharaja Forest Dynamic Plot (FDP). It is a 25-ha FDP and located in the lowland rain forest of the

Sinharaja which is an UNESCO World Heritage Site at the centre of the ever-wet south-western region of Sri Lanka (6° 21-26'N, 80° 21-34'E). It was established in 1993 by the University of Peradeniya and the Forest Department of Sri Lanka. Sinharaja FDP spans the elevational range of 424 m to 575 m above sea level. In Sinharaja 18,065 adults were found (trees with diameter of breast height ≥ 10 cm), belonging to 188 species. (Census year-1996)

2.2 Data set

The empirical SAR was constructed using data from Sinharaja FDP which was initiated in 1996. The data set contains 20 variables but only few of them are considered for this study (species name-sp, spatial coordinates (gx, gy), 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) 10 cm as adult trees. Therefore, we also used all the trees with dbh 10 cm in the Sinharaja FDP as adult trees. Although this threshold value is crude it is useful for cross site comparisons.

θ 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) ≥1 cm and dbh ≥10 cm. For this study, only the trees with dbh ≥ 10 cm were considered from the latest census of each FDP.

2.3 Neutral model and species area curve for 25ha Sinharaja forest plot

We simulated neutral communities (see Etinne, 2009; Hubbell, 2001; Hubbell, 1996) for various and m combinations. The number of individuals in the neutral community (J) was fixed and it was the community size of the Sinharaja FDP. For each and m combination species richness (S_n) was calculated. The neutral theory assumes that community is saturated. Thus, number of individuals in a local community (J) is proportional to the area (A) sampled (i.e.J=ρA).

Species richness versus area sampled was plotted for the best θ and m combination. (This is the graphical representation of SAR). We constructed empirical SAR and SAR based on the neutral model. (1) Empirical SAR was constructed by throwing a quadrate 99 times randomly and calculating the average species richness. (2) Step-1 was repeated 99 times (99 simulations) to construct the simulation envelope for the empirical SAR. (3) Size of the quadrate was changed to increase the area sampled. Correction to the edge effects was also used. The statistical analysis was conducted using R software (R Core Team, 2014).

3 RESULTS AND DISCUSSION

Figure 1 shows the species richness (S) for various and m combinations with fixed local community size (J=18,065). We found that when = 36 and m=0.14 species richness of the neutral community (187) is very close to the species richness of the Sinharaja forest plot (188). Figure 2 shows species richness vs. community size (J); sampled for Sinharaja forest plot ($J = \rho A$) (black line) and its 95% simulation envelope (shaded gray). We noticed that SAR under the fully neutral model (red line in Figure 2) is inside the 95% confidence interval of the empirical SAR. This indicates that the neutral model can explain empirical SAR of the Sinharaja forest.

We considered species abundance tables (for trees with dbh 10 cm) for nine other large forest plots (Web: Smithsonian Tropical Research Institute-http://www.forestgeo.si.edu/) and

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estimated and m values for these forest plots (Table 1). When species richness is low and/or m is low. Mudumalai (in India) and Yasuni (in Ecuador) show lowest and highest values respectively. (Table 1)

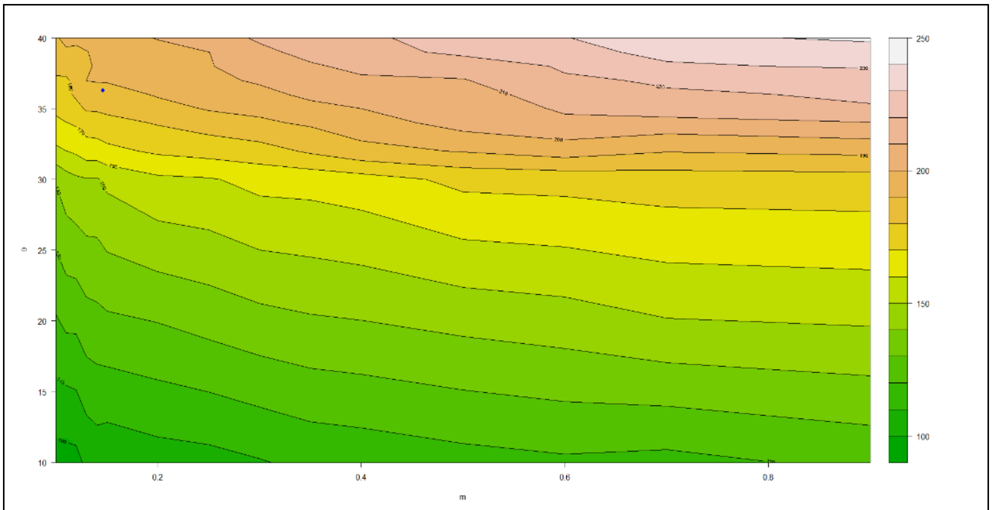

Figure 1: Species richness for various θ and *m* combinations with fixed local community size (*J=18,065*). J= All the trees, dbh ≥ 10 cm, in the Sinharaja FDP. Blue solid dot represents the species richness of Sinharaja (188) and its θ=36 and *m*=0.14.

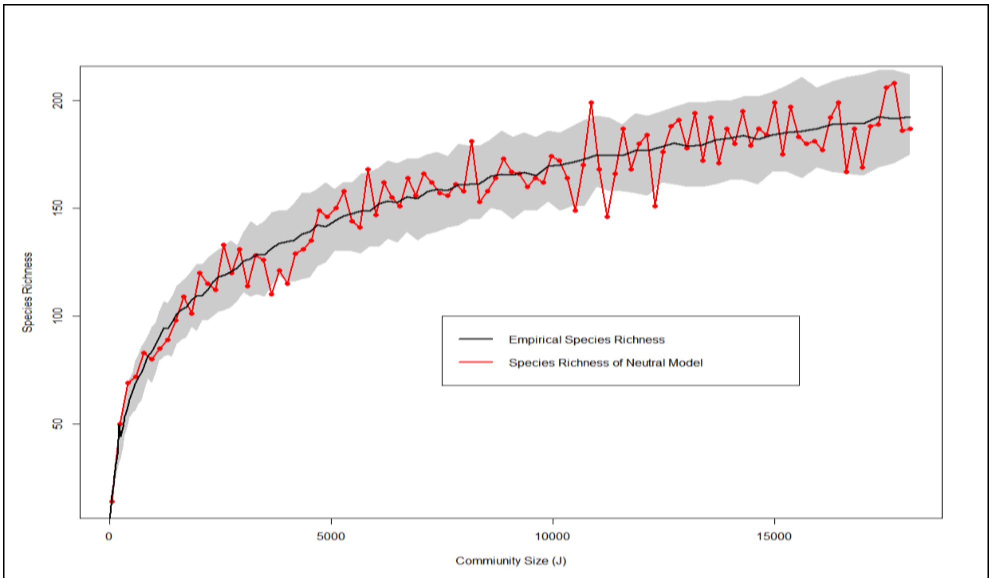

Figure 2: Species richness vs. community size (*J*); sampled for the 25-ha Sinharaja FDP ($J = \rho A$) (black line), its 95% simulation envelope (shaded gray). SAR under the neutral model (red line).

Table 1: θ and m combination for 10 forest dynamic plots in Centre for Tropical Forest Science (CTFS).

Study Plot (Country)	Study area (ha)	Community Size (yr.) (J)	Species Richness (S)	θ	m
BCI (Panama)	50	20848 (2005)	227	50	0.10
EDORO (Africa)	10×2	9382 (2000)	207	52	0.12
FUSHAN (Taiwan)	25	19270 (2002)	77	15	0.03
KORUP (Africa)	50	24591 (1998)	308	66	0.12
LAPLANADA (Colombia)	25	15013 (2003)	173	35	0.14
LENDA (Africa)	10×2	7300 (2000)	213	58	0.13
MUDUMALAI (India)	50	12579 (2000)	61	14	0.02
PASOH (Malaysia)	50	28279 (2000)	671	180	0.10
SINHARAJA (Sri Lanka)	25	18065 (1996)	188	36	0.14
YASUNI (Ecuador)	50	17434 (2003)	819	259	0.15

We observed that the neutral model with m=0.14 and θ=36 can explain the species richness of the Sinharaja FDP. Hubbell (1997) found that, m=0.1 and θ=50 for Barro-Colorado Island (BCI) in Panama and m=0.15 and θ=180 for Pasoh forest in Malaysia. It was found that the m value of the Sinharaja forest (m=0.14) is higher than the BCI value (m=0.1) and smaller than Pasoh value (m=0.15). Perhaps, trees in the Sinharaja forest are taller than trees in the BCI forest but shorter than the trees in the Pasoh forest. This should be the reason for the above result. However, we could not construct the empirical SAR for these nine forest plots since the spatial arrangement (gx,gy coordinates) of these forest plots were not available.

4 CONCLUSIONS AND RECOMMENDATIONS

Our findings indicate that the neutral model (which does not consider the habitat association, dispersal syndrome of species, Janzen-Connell effects, species interactions and their joint effects) can explain the SAR of the Sinharaja forest plot. This emphasizes that the spatial arrangement of species are not important to describe the large scale patterns. Also the estimated θ and m values proved that, when species richness is low θ and/or m is low.

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