Roles of Different Nearly Neutral Models in Maintaining Species Coexistence of Tropical Forests

T.L.M. Ruberu[1]*, I.A.U.N. Gunatilleke[2], C.V.S. Gunatilleke[2] and R. Punchi-Manage[1]

[1]Department of Statistics and Computer Science, University of Peradeniya, Sri Lanka
[2]Department of Botany, University of Peradeniya, Sri Lanka

Corresponding author: Email: laksru21@gmail.com

1 INTRODUCTION

One of the central issues in ecology is the question of species coexistence. It has been found that the ecosystems of the world contain a remarkable diversity of species. Out of these, tropical forests are high in species richness compared to other forests. Dozens of theories have been proposed to explain the possible mechanisms of species coexistence. (Hubbell, 2001, Seidler and Plotkin, 2006, Wright *et al.,* 2002). But this question still does not have a specific answer which is agreed upon. The recently introduced Hubbell's neutral theory (Hubbell, 2001) provides a new framework for this debate. Neutral theory considers the community to be saturated and the species to be functionally equivalent (Hubbell, 2006, Hubbell, 2001).Functional equivalence implies that all the individuals have same dispersal abilities, birth rates and death rates. The originally proposed Hubbell's neutral theory is spatially implicit and assumed unlimited dispersal ability of species. That is, once an individual dies, the vacant site is occupied by any individual of the local community with probabilities equal to the post abundances of species in the local community. However Assumptions of the neutral theory were strongly criticized by supporters of the niche theory. They argued that species are different with respect to their birth, death rates and dispersal abilities.

A crucial factor that is used to assess species coexistence is species richness Species richness gives the total number of species recorded in an area at a given time. Higher species richness cause heterogeneity and stabilize the ecosystem. This study is focused on identifying a nearly neutral model that is a variant of the neutral model which facilitates high species coexistence than the neutral model in terms of species richness. With this purpose (1) four nearly neutral models are simulated where each model relax a subset of assumptions in the neutral model (equal death rates, equal dispersal ability) and species richness values after 50 years under each nearly neutral model was compared with that of the neutral model. (2) Point patterns of species after 50 years under all models were studied. However this study does not consider the speciation rates and assumes the community is isolated. Thus no new species originate through evolution and species do not migrate to the community from outside. It is of utter importance to preserve the diversity while we dominate this planet since the cost of replacing the services provided by this diversity if possible would be extremely expensive. For this cause identifying the mechanisms that ensure species coexistence is of extreme importance.

2 METHODOLOGY

2.1 Study Area

We considered data from all the species in the $500m \times 500m$ fully mapped Sinharaja forest plot (Sri Lanka). In the plot large trees of all the species were considered. The 99th percentile of ranked dbh values for all the trees of each species were determined and 93,593 trees with a dbh $\geq$ dbh (99) [2/3], representing 238 species were considered as adults (Bagchi *et al.,* 2011).

2.2 Composition of the Dataset

The dataset for empirical data was collected by a collaboration between Centre for Tropical Sciences and Department of Botany, University of Peradeniya. Two censuses of the dataset taken at five year time intervals (1996, 2001) were used for the study. The variables used were Tree ID (used to uniquely identify every individual tree), species name, spatial coordinates, diameter at breast height and whether a tree is dead or alive at the time of census.

Table 1: Description of the Models

Model	Assumption Relaxed	Selection of Death Tree	Replacement
Neutral model	Null	Random	Replacement occurred with constraint
Euclidean distance model	Assign species specific limited dispersal abilities through Euclidean distance method	Random	Euclidean distance between death and random trees (d) was determined. Replacement occurred only if d did not exceed dispersal threshold value of recruit species
Kth nearest neighbour distance model	Assign species specific limited dispersal abilities through Kth NN distance method	Random	Euclidean distance between death and random trees (d) was determined. Replacement occurred only if d did not exceed dispersal threshold value of recruit species
Unequal death rates model	Assign different death rates for species	Subject to death probabilities	Replacement occurred without constraints
Unequal death rates and dispersal limited model	Assign species specific limited dispersal abilities through Kth NN distance and death rates	Subject to death probabilities	Euclidean distance between death and random trees (d) was determined. Replacement occurred only if d did not exceed dispersal threshold value of recruit species

2.3 Models of the Study

Death rate of trees in Sinharaja forest plot was calculated for a 5yrs., period (mortality =6956) using the data from first two censuses. To relax a subset of the assumptions in the neutral model, species specific dispersal threshold values and

birth, death rates were assigned to species. Two methods were employed to compute different dispersal threshold values for species. (1) Obtaining the matrix of the Euclidean distance between each pair of conspecific trees and taking their average. (2) Measuring 100th nearest conspecific neighbour distance from each tree

belonging to a given species and averaging thus obtained values. In both these methods singletons (Species with only one tree) were given unlimited dispersal ability. The probability of death of a given species (d_j) was computed using $d_j = i$/mortality rate, where i is the number of dead trees after 5 yrs., of jth species. In each of the following

models two trees from the plot were selected as death tree and the recruit tree (Recruit tree was always randomly selected). The vacant site was then replaced by the recruit tree. However the selection of two trees and replacement occurred subject to constraints considered under each model. Species richness was recorded after every five years for 50 years.
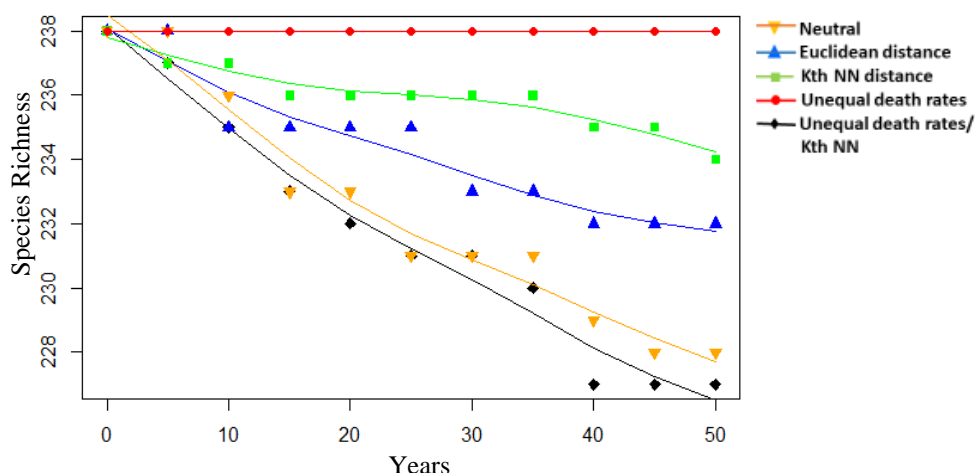
3 RESULTS AND DISCUSSION

Figure 1: The species richness curves of the models

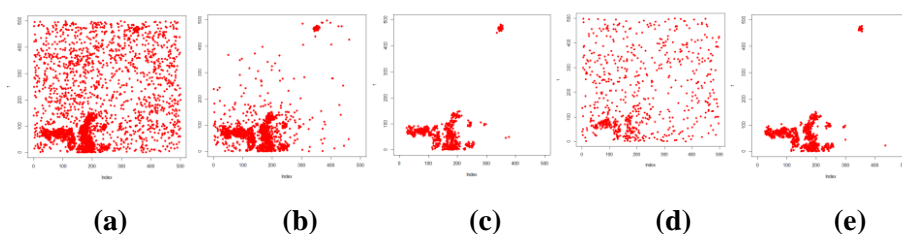| **(a)** | **(b)** | **(c)** | **(d)** | **(e)** |

Figure 2(a)-(e): The spatial arrangement of one of the species "*AGROHO*" after 50 yrs under five different models. (a) Neutral Model (b) Euclidean distance (c) K^th^-nn distance (d) Unequal death rates (e) Unequal death rates and K^th^-nn distance

The species richness of the neutral model was lower than that of the dispersal limited models after 50 yrs. Species that have limited dispersal ability cannot reach all the favourable sites. Therefore, limited

dispersal ability of species can delay species extinction and mono-dominance. However it is observed that the model which employed K^th^ nearest neighbour distance to assign dispersal threshold

values performed considerably well than the Euclidean distance model. In tropical forests many species are aggregated into several clusters (Seidler and Plokin 2006; Plotkin et al. 1996) .When computing the Euclidean distances between each pair of conspecific trees both inter cluster and intra cluster distances are considered. If two clusters of conspecific trees are located at opposite corners of the plot this might result in very high distances yielding high dispersal threshold values for species. On the other hand it is less probable for 100th conspecific neighbour to be in a distinct cluster. Hence assigned dispersal threshold values for species are low. This might be the reason for the species richness values of Euclidean distance model to fall in close proximity with that of the neutral model. Further the singletons were assigned unlimited dispersal ability. This assumption leaves an advantage for the rare species. However this advantage could be ecologically justified considering low density dependent effects of rare species.

The model that considers death rates conserves species richness at initial level. This work allows us to study separate effects of dispersal limitation and different death rates. However it was found that many species were extinct during the period of 50 yrs., when species have unequal death rates and limited dispersal abilities .This result is surprising because niche theory assume that species differences such as death rates and dispersal ability can contribute to maintain the species richness. Species interactions might be the reason behind this.

There were 238 species in the Sinharaja forest plot. Spatial arrangements of a few dominant species were plotted initially and after 50 yrs., under the neutral and nearly neutral models. It was evident that the initially clustered conspecific trees were scattered afterwards. This provides further evidence that the dispersal limited species cannot reach the preferred sites.

4 CONCLUSIONS AND RECOMMENDATIONS

Species coexistence can be better explained when moving away from strict neutrality. Assigning different dispersal threshold values for species contribute in maintaining species richness. However these affects are insignificant unless strong dispersal limitations are considered. It is evident that dispersal limitation and death rate alone can explain high species richness and the neutral model has oversimplified assumptions that are not realistic. However adding more complexity decreases the performance of the model. Therefore the best model is not a simple model nor a very complex model but a moderate model. The model with different death rates best preserved the species richness. Hence this model could be identified as the best model that explains the species coexistence in terms of species richness maintenance. This study provides some evidence to support the preservation of the spatial arrangement of species

REFERENCES

Bagchi, R., Henrys, P., Brown, P., Burslem, D., Diggle, P., Gunatilleke, C., Gunatilleke, I., Kassim, A., Law, R., Noor, S. and Valencia, R. (2011). Spatial patterns reveal negative density dependence and habitat associations in tropical trees. *Ecology*, 92(9), pp.1723-1729.

Hubbell, S.P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology,* **87***,* 1387–1398.

Hubbell, S.P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Seidler, T.G. and Plotkin, J.B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, e344.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia, 130,* 1–14.v