

Are Diamond's assembly rules applicable to tropical threatened vascular plants assemblages in the Tarap Hill Reserve in Bangladesh?

(Submitted : 17.04.2020 ; Accepted : 28.06.2020)

Mahmuda Sharmin^{1,2*}, Swapan Kumar Sarker¹

¹Department of Forestry and Environmental Science, Shahjalal University of Science & Technology, Sylhet-3114, Bangladesh

²Hawkesbury Institute for Environment, Western Sydney University, Richmond, NSW- 2753, Australia

*Corresponding author's email m.sharmin@westernsydney.edu.au

Abstract

Disentangling the co-existing patterns (random or non-random) of species and to infer about assembly rules underpinning the observed patterns are central research issues in community ecology. Previous empirical results suggested that Diamond's assembly rule explains a considerable amount of observed species spatial distribution pattern variation. However, the rule has yet to be checked in tropical forests where plant communities experience high anthropogenic disturbances and rapid conversion of natural forests has resulted in fragmented forests with many threatened species. In this study, we collected the occurrence data of both red-listed and general vascular plant species from four distinct forest types (e.g., undisturbed natural, disturbed natural, matured secondary, and mixed plantation forest) in Tarap Hill Reserve, Bangladesh. Our results comply with the basic predictions of Diamond's assembly rules in threatened vascular plants assemblages in undisturbed natural and matured secondary forests, and at the forest landscape level as well. Conversely, we observed random co-occurrence patterns at disturbed natural and managed mixed plantation forests. In conclusion, our results indicate that although competition plays a pivotal role in structuring tropical threatened plants assemblages at different forest types and the forest landscape level, anthropogenic disturbances also have strong influences upon threatened species distribution.

Keywords: Competition; null models; disturbance; presence-absence matrix; Bangladesh.

1. Introduction

Investigating the principle processes (e.g., non-random or random) that assemble plant communities has been a significant trend in community ecology. These investigations have been producing contrasting results. Clements [1] and Phillips [2] supported non-random processes viewing plant communities as "complex organisms" that do not assemble randomly but rather exist in certain combinations. In contrast, Gleason [3] supported random processes stating "an association is not an organism, scarcely even a vegetational unit, but merely a coincidence". Furthermore, Hubbell's unified neutral theory denies the uniqueness of the species, rather assumed that each species follows a random walk and in a particular trophic level they have the same chance of reproduction and death, regardless of their identity [4]. This debate has not resolved yet and ecologists are still searching for principle processes that structure communities [4-14]. With the advancement of statistical and mathematical tools in ecology, species co-occurrence analyses are soaring up to assess the community assembly processes. Many

studies tried to evaluate whether the assemblages are due to random assemblages of species [15, 16], or deterministic mechanisms such as competition [17-19], or habitat heterogeneity [20, 21], or species turnover [22]. A primary objective of these analyses is to find out the evidence for Diamond's assembly rules [23]. Diamond identified that competition for foraging resources among fruit-eating birds in the New Guinea archipelago lead to their non-randomly structured assemblages [23]. However, Connor and Simberloff challenged Diamond's approach and argued for random species co-occurrence patterns [24]. Since then the community assembly rules of Diamond sparked a contentious debate questioning the scientific validity of assembly in nature [17, 25, 26].

Gotelli and McCabe showed that in nature non-random co-occurrence patterns seem to exist [18]. Their results also suggested that Diamond's assembly rule explained a considerable amount of variation in species' spatial distribution patterns. However, Götzenberger et al. have asserted that in nature, particularly in plants, non-random co-occurrence is not a widespread phenomenon [6].

The Diamond's assembly rules have been famously assessed for avian communities [23, 27, 28], ants [29], mammals [30], spiders [31] and beetles [10]. Although plants have been considered as the most important taxon to explore the patterns in community ecology, little attention has yet been paid to them [32-34]. Tropical plant communities even received less focus than the temperate plant communities although tropical forests have phenomenal plant diversity with 24% of the world's endemic plants [35,36].

Historically, worldwide forests are subjected to high anthropogenic [37] and climatic disturbances [38, 39]. Most of the primary tropical forests have been converted to different fragmented forest types (e.g., secondary forests, mono or mixed plantations, etc.). These forest types are often rich in threatened species diversity and have become vital habitat refugia for conserving threatened species [40, 41]. Although it is documented that natural disturbances reduce the strength of competitive exclusion among plants and result in random co-occurrence patterns of neighboring species [42]. However, we are unaware of any work that assessed the assembly rule model of Diamond on threatened plants assemblages of tropical forests. In fact, examining assembly rules in the threatened plant assemblages of the different fragmented forest types along with the entire plant communities is crucial because this will help us to predict plant responses under changing environmental conditions.

This paper seeks to investigate the co-occurrence patterns in the vascular plant communities of the tropical Tarap Hill Reserve in Bangladesh. We focus on both common and threatened vascular plant assemblages in the natural (undisturbed and disturbed), secondary and mixed plantations forest in the reserve. First, we hypothesized that Diamond's assembly rules are applicable to tropical threatened vascular plant assemblages. Secondly, the plant assembly patterns in the disturbed and plantation forests will deviate from the natural forests due to human intervention.

1. Methodology

2.1. Study areas and species survey

The study was carried out in the tropical Tarap Hill Reserve (6,232 km², 24°06' to 24°14'N latitude and 91°34' to 91°41' E longitude) Bangladesh [43]. The reserve is located along the Bangladesh-India border in Chunarughat Upazila of Habiganj district and is a part of the Indo-Burma Biodiversity Hotspot [44]. This part of the country enjoys a moist tropical climate with a mean annual temperature is 25.8°C with high seasonal variation (with an average temperature in winter months is 10°C and range of 30 - 40°C temperature in summer months [44]. Yearly precipitation could be up to 2371.7 mm most of which occurs between May and July [44].

Once covered by natural patches, vegetation composition of the reserve has substantially changed because of severe

anthropogenic disturbances and management practices [45]. At present, the reserve comprises mainly three tropical semi-evergreen forest types: (I) natural (undisturbed and disturbed), (II) mature secondary and (III) mixed plantation forests. These forests contain critical habitats of red-listed vascular plants [46].

The reserve comprises three forest beats i.e. Chanbari, Kalenga, and Rema (Figure 1). Natural forests of the reserve fall under the Rema-Kalenga Wildlife Sanctuary (RKWS) which is the largest upland sanctuary (19.76 km²) in Bangladesh [47]. Kalenga site of the sanctuary is mostly free of anthropogenic disturbances and comprises the undisturbed natural forest. Chanbari site comprises the disturbed natural forests which have been subjectively disturbed by illegal logging, fuelwood collection and grazing and agricultural extension and settlement for several hundred years [48,44].

The mature secondary forests and plantation forests are located in or around the natural forests. The mature secondary forests were planted with native species (eg. *Dipterocarpus turbinatus*, *Michelia champaca* and *Shorea robusta*) and have not received any sort of management during the last 50 years. Therefore, native vegetation could regenerate and coexist with the planted trees. In contrast, plantation forests are comparatively new establishments and are mainly dominated by *Acacia auriculiformis*, *Acacia mangium* and *Tectona grandis*.

2.2 Sample size

Quantitative vegetation surveys were conducted in a total of 175 sample plots (undisturbed natural forest = 50 plots, disturbed natural forest = 25 plots, matured secondary forest = 50 plots, and mixed plantation forest = 50 plots) of 20 x 20 m² each at random in our four study forests from August 2010 to February 2012. We carried out a comprehensive species survey in each plot where most species were identified to species level with the help of field assistants and the remaining species were collected and identified with the key [49]. We only surveyed vascular plants. by chance [52]. For each matrix, we calculated the observed index and then compared it with the index for 10000 randomly assembled null communities. We used row sum fixed-column sum fixed (SIM9 of Gotelli [51]) null algorithm for measuring C-score and checkerboard pairs. In this algorithm, both the row and column sums of the original matrix were fixed; so that differences in the frequency of occurrence of each threatened species (row sums) and differences in the number of threatened species per sample plot (column sums) were preserved [24]. Although this algorithm was criticized, Gotelli [51] identified good strength of this algorithm in measuring the C-score and the number of checkerboards. We created null matrices with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 [53]. Co-occurrence analysis and associated randomization tests were performed by using null model software Ecosim 7.72 [54].

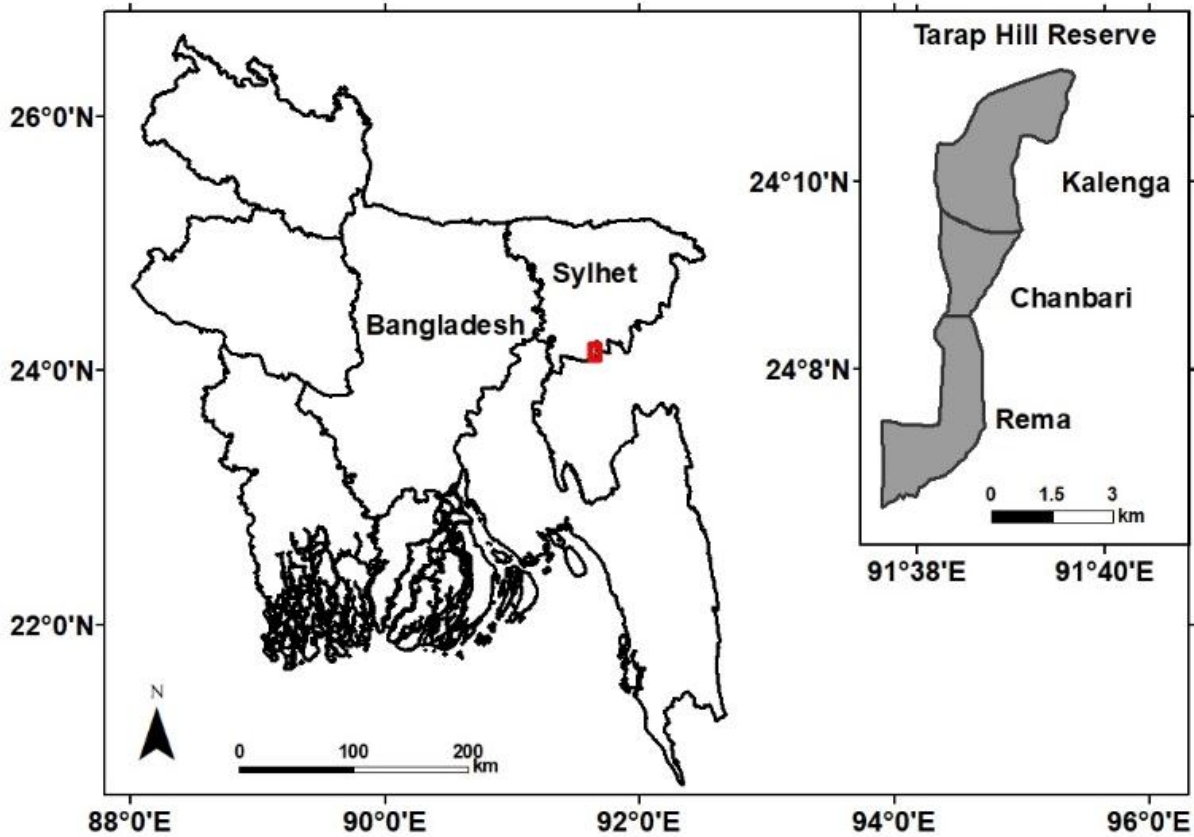


Figure 1: The red dot on the map of Bangladesh indicates the location of Tarap Hill Reserve. The insert depicts a detailed map of Tarap Hill Reserve forest with the three forest beats. The present study was undertaken in Kalenga and Chanbari forest beats of Tarap Hill Reserve forest.

2.3. Data analysis

To quantify Diamond’s assembly rules [23], we used species presence-absence matrices. The Red Data Book of Bangladesh [50] has enlisted 106 red-listed vascular plants and we checked out the list of recorded species in our study against the Red Data Book. For each studied forest type, we constructed two presence-absence data matrices: (i) full species occurrence dataset (both red-listed and non-red-listed species) and (ii) threatened species occurrence dataset (only red-listed species). Later, we pooled the full species datasets and threatened species datasets to attain two separate datasets for computing co-occurrence patterns at the forest landscape level. In each presence-absence matrix, rows represent species and columns represent the presence (1) or absence (0) of species in samples (or sites) [14].

We used two co-occurrence indices to calculate and compare the co-occurrence patterns of all species and the threatened species at four studied forest types and also at the forest landscape level. These indices include: (I) the number of species pairs forming perfect checkerboards (CHECKER) [23] - describe Diamond’s fifth assembly rule: “some pairs of species never co-exist, either by themselves or as a part of a larger combination” (1975:344) (II) the checkerboard score (C- score) [22] - related to CHECKER but not as stringent as the

measurement of CHECKER. The checkerboard index was calculated by counting the number of unique pairs of species that never coexist [18]. Equation 1 was used to calculate C-score for each pair of species. This C-score value is the average of all possible pairs of species in the presence-absence matrix. The number of species

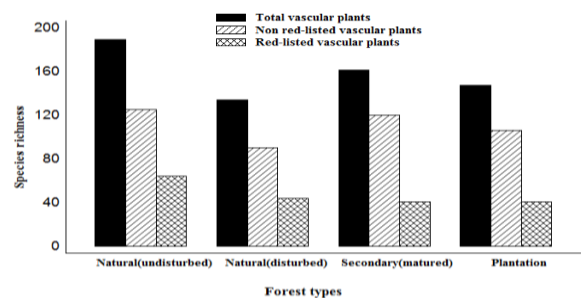


Figure 2. Species richness in the fragmented forest types of Tarap Hill Reserve, Bangladesh.

combinations are calculated by counting the number of distinct arrangements represented by the columns of the matrix

$$(R_i - S)(R_j - S) \tag{1}$$

where R_i and R_j are the matrix row totals for species i and j , and S is the number of sites in which both species occur [18].

3. Results

To test and identify the statistical difference of observed assembly patterns a null model was performed [18,51]. In null model tests, the statistical properties and performance of these indices were well described in Gotelli [51] and Gotelli and McCabe [18]. If an assemblage is structured by competition, observed communities should contain a larger C score and more checkerboard pairs than expected

3.1. Vascular plant diversity

The vegetation survey in different forest types in the Tarap Hill Reserve yielded 230 vascular plant species of 57 families, of which 72 species of 37 families were categorized as red-listed species (Table 1), Global status

of the majority of these red-listed species have not yet been checked by IUCN except few (e.g., *Aquilaria agallocha* Roxb.; *Mangifera sylvatica* Roxb.; *Chukrasia tabularis* A. Juss. and *Shorea robusta* Gaertn [55]). We recorded the highest number of red-listed (64) and non-red-listed (125) vascular plants from the undisturbed natural forest (Figure 2).

Conversely, the disturbed natural forest has the lowest species (both red-listed and non-red-listed plants) richness. Except for undisturbed natural forest, red-listed species richness is quite similar in the other three forest types.

Table1. Threatened species sampled in Tarap Hill Reserve. Forest type 1= undisturbed natural forest; forest type 2= disturbed natural forest; forest type 3= matured secondary forest and forest type 4= mixed plantation forest.

Family	Scientific Name	Local name	Forest types
Alangiaceae	<i>Aquilaria agallocha</i> Roxb.	Agar	1
Anacardiaceae	<i>Mangifera longipes</i> Griff.	Milum	1,2
	<i>Mangifera sylvatica</i> Roxb.	Milum	1
	<i>Spondias pinnata</i> (L.f.) Kurz	Amra	1
	<i>Semicarpus anacardium</i> L.f.	Bhela	1,2,3
	<i>Holigarna longifolia</i> Roxb.	Barala	1,4
Apocynaceae	<i>Alstonia scholaris</i> L.	Chhatim	1,2
	<i>Rauvolfia serpentina</i> (L.) Benth. ex Kurrz	Sarpagandha	1
	<i>Willughbeia edulis</i> Roxb.	Lolam	1,2,4
Araceae	<i>Homalomena aromatica</i> Schott	Gandhakachu	1,3
	<i>Stuednera colocasiodes</i> Hook.f.	Bishkachu	1,3,4
	<i>Aglaonema hookerianum</i> Schott	Bankachu	1,2,3,4
Arecaceae	<i>Calamus tenuis</i> Buch.-Ham. ex Martius	Khumbhi	1,2,3,4
	<i>Daemonorops</i> .	Jali bet	1,2,3,4
	<i>Didymosperma nana</i> H. Wendl. & Drude.	Banmurta	1,2,4
	<i>Licuala peltata</i> Roxb.	Satipata	1,3
Asclepiadaceae	<i>Hoya parasitica</i> Wall.	Cerapata	1,2
Asteraceae	<i>Adhatoda zeylanica</i> Medikus	Basak	1,2,3,4
Bignoniaceae	<i>Oroxylum indicum</i> Vent.	Thona	1,2,3,4
Bombacaceae	<i>Bombax insigne</i> Wall.	Toirol	1,2
Caesalpinaceae	<i>Cassia fistula</i> L.	Bandarlathi	1
	<i>Cassia nodosa</i> F. Ham. ex Roxb.	Bansunalo	1
Cluciaceae	<i>Garcinia cowa</i> Roxb.	Kao	1
	<i>Garcinia xanthochymus</i> Hook.f. ex T. Ander	Dephal	1,2
Combretaceae	<i>Terminalia bellirica</i> Roxb.	Bohera	1,2,3,4
	<i>Terminalia citrina</i> Roxb.	Horitoki	1,2,3,4
Dilleniaceae	<i>Dillenia indica</i> L.	Chalta	1
Dioscoreaceae	<i>Dioscorea prazeri</i> Prain and Burkill	Banalu	1,3,4
Dipterocarpaceae	<i>Shorea robusta</i> Gaertn.	Sal	1,2,3,4
Elaeocarpaceae	<i>Elaeocarpus robustus</i> Roxb.	Belpoi	1,2,3,4
Euphorbiaceae	<i>Antidesma ghaesembila</i> Gaertn.	Anna	1,2,3,4
	<i>Baccaurea ramiflora</i> Lour.	Bhubi	1,2

	<i>Macaranga denticulata</i> Muell.-Arg.	Bura	1,3
	<i>Macaranga indica</i> Wight	Gulile	1,2,3,4
	<i>Macaranga peltata</i> Muell.-Arg.	Nainna bichi gash	1,2,3,4
	<i>Phyllanthus emblica</i> L.	Amloki	1,2,3,4
	<i>Bridelia Stipularis</i> (L.) Bl.	Harinhara	1
Fabaceae	<i>Butea roxburghii</i> Benth.	Hatilata	1,2,3,4
Fagaceae	<i>Castanopsis indica</i> (Roxb.) Miq.	Hingra	1,2,3,4
Lauraceae	<i>Litsea glutinosa</i> (Lour.) C.B. Robinson	Menda	1,2,3,4
	<i>Litsea panamonja</i> Buch.-Ham.	Chita	1,2,3,4
Mimosaceae	<i>Entada phaseoloides</i> (L.) Merr.	Gila	1,2,3,4
Liliaceae	<i>Crinum defixum</i> Ker.	Gorun	1,2,3,4
Meliaceae	<i>Chukrasia tabularis</i> A. Juss.	Chukrasi	1,2,4
Menispermaceae	<i>Pericampylus glaucus</i> (Lamk.) Merr.	Goallata	1,2,3,4
	<i>Tinospora crispa</i> (L.) Hook.f. & Thoms.	Amguruz	1,4
Mimosaceae	<i>Albizia lebbek</i> (L.) Benth.	Koroi	1,2,3,4
	<i>Albizia lucida</i> Benth.	Shilkoroi	1,2,3,4
Moraceae	<i>Ficus glomerata</i> Roxb.	Jogdumur	1,2,3,4
	<i>Ficus recemosa</i> L.	Pakur	1
	<i>Ficus religiosa</i> L.	Ashwath	1
Musaceae	<i>Musa rosacea</i> Jacq. (<i>M. ornate</i> Roxb.)	Ramkola	2,3,4
Myrtaceae	<i>Syzygium wallichii</i> (Wight) Walp.	Ajam	1,2
Orchidaceae	<i>Cymbidium aloifolium</i> (L.) Gw.	Porgacha	1,2,3
	<i>Vanda teres</i> (Roxb.) Lindl.	Talachabi	1,2,4
Poaceae	<i>Oryza granulata</i> Nees et. Arn. ex Steud.	Bansdhan	1,2,3
	<i>Oryza latifolia</i> Desv.	Bondhan	1,2,3,4
Rubiaceae	<i>Neonauclea sessilifolia</i> (Roxb.) Merr.	Kutikadam	1,2,3,4
	<i>Paedaria foetida</i> L.	Gandhaveduli	1
Rutaceae	<i>Zanthoxylum rhetsa</i> (Roxb.) DC.	Bazna	1,3
Sterculiaceae	<i>Pterospermum acerifolium</i> Willd.	Moskand	1,2
	<i>Sterculia villosa</i> Roxb.	Chandul	1,2,3,4
Vaticaeae	<i>Vitis quadriangularis</i> Wall.	Harbhanga lata	1,2
Lecythidaceae	<i>Careya arborea</i> Roxb.	Khumbi	1,3,4
Verbenaceae	<i>Gmelina arborea</i> Roxb.	Gamari	1,3
	<i>Vitex diversifolia</i> Kurz	Awals	1,2,3,4
	<i>Vitex peduncularis</i> Wall. ex Schauer.	Awals	1,2,3,4
	<i>Vitex pubescens</i> Vahl	Teliawal	1,2,3,4
Zingiberaceae	<i>Amomum aromaticum</i> Roxb.	Tara	1,2,3,4
	<i>Amomum corynostachyum</i> Wall.	Tara	1,2,3,4
	<i>Hedychium thyrsoforme</i> Buch.-Ham ex Smith	Banada	1,3,4
	<i>Curcuma amada</i> Roxb.	Ada	3

3.2. Co-occurrence patterns

3.2.1. Undisturbed natural forest

The fixed-fixed null model algorithm (SIM9) asserts clear evidence of non-random co-occurrence patterns of the Table 2. Summary of the null model tests for the co-occurrence indices- CHECKER and C-score. Null models calculated the statistical differences between observed and randomized community assemblage patterns of common and threatened species occurrence datasets of different forest types and at the forest

landscape level. ^a observed; ^b expected; *P* the significance level for the test of the null hypothesis; NS not significant (*P* > 0.05); UNF=Undisturbed natural forest, DNF = Disturbed natural forest, MSF = Matured secondary forest, MPF = Mixed plantation forest, and FLL= Forest landscape level. entire vascular plant community and the threatened plants within the undisturbed natural forest. The observed C-scores for full species occurrence dataset (26.40) and threatened

Co-occurrence Indices	Full species occurrence datasets					Threatened species occurrence datasets					
	UNF	DNF	MSF	MPF	FLL	UNF	DNF	MSF	MPF	FLL	
Obs ^a	26.40	5.72	7.64	4.20	63.20	78.44	6.51	47.34	3.44	98.85	
C-score	Exp ^b	26.13	5.86	7.55	4.14	62.64	76.68	6.68	45.89	3.58	92.60
	<i>p</i>	0.01	NS	0.02	0.01	0.01	0.01	NS	0.01	NS	0.01
Obs ^a	9150.00	900.52	8553.00	7145.0	24026	1004	564.0	516.0	577.0	1330.00	
CHECKER	Exp ^b	9090.11	933.00	8342.25	7067.97	23444	959.81	569.42	498.0	576.16	1320.66
	<i>p</i>	0.04	NS	0.01	0.01	0.01	0.01	NS	0.01	NS	0.03

species occurrence dataset (78.44) are significantly larger than the mean of simulated C-scores which are 76.68 ($\pm 0.24\sigma$ and $P = 0.00$) and 26.13 ($\pm 0.044\sigma$ and $P = 0.00$) respectively (Table 2). The observed checkerboard units for full species dataset (9150) and threatened species dataset (1004) are also significantly higher than the mean of simulated checkerboard units which are 9090.11 ($\pm 33.205\sigma$ and $P = 0.04$) and 959.81 ($\pm 19.27\sigma$ and $P = 0.01$) respectively.

3.2.2. Disturbed natural forest

We observe random species co-occurrence patterns in the disturbed natural forest. For both full species dataset and threatened species dataset, the observed C-scores (5.72 and 6.51) and checkerboard units (900.52 and 564.00) are smaller than the average of simulated values (C scores: 5.86 and 6.68; checkerboard units: 933.00 and 569.42).

3.2.3. Matured secondary forest and mixed plantation forest

The results of the indices (C-score and CHECKER) vary for the matured secondary and mixed plantation forest types. The observed C-scores and checkerboard units for full species dataset and threatened species dataset of the matured secondary forest is significantly larger than the simulated mean values indicating non-random co-occurrence pattern. However, the values of the indices show a random co-occurrence pattern for both full species datasets and threatened species datasets at mixed plantation forests.

3.2.4. Forest landscape level

At the forest landscape level, species co-occurrence pattern in both the entire community and the threatened assemblages within it shows consistency with Diamond's assembly rules. The observed C-scores for pooled all species dataset (63.20) and pooled threatened species dataset (98.85) are significantly higher than the mean of simulated C-scores which are 62.64 ($\pm 0.1\sigma$ and $P = 0.00$) and 92.60 ($\pm 0.51\sigma$ and $P = 0.00$) respectively. The observed checkerboard units for pooled all species dataset (24026) and pooled threatened species dataset (1330.00) are also significantly larger than the mean of simulated checkerboard units, 23444 ($P = 0.00$) and 1320.66 ($P = 0.03$) respectively.

4. Discussion

The present study showed that Diamond's assembly rules are broadly applicable in the plant communities in the Tarap Hill Reserve in Bangladesh, which implies tropical vascular plant communities exhibit non-random co-occurrence patterns. At the forest landscape level and all forest types (undisturbed natural, matured secondary, and mixed plantation forest types) except disturbed natural forest vascular plants exhibited non-random co-occurrence patterns. Our finding denies the functionality of randomness of species occurrence in ecological communities, thus in contrast with Hubbell's neutral theory [13], which ignores the uniqueness of species, their different ability to use resources and evolutionary history.

The tropical threatened plants assemblages within these communities exhibit non-random co-occurrence patterns at the landscape level and at the undisturbed natural and mature secondary forests. However, in the disturbed

natural forest, both the entire community and the threatened assemblages show random co-occurrence patterns. This finding validates our second hypothesis that the community assemblage patterns of disturbed natural and secondary forest deviate from the natural forest, due to human intervention

In the undisturbed natural forest, like the entire community, strong interspecies competition may also exist within the threatened assemblages and can result in non-random species assemblages (larger C-score and more Checkerboard pairs than expected by chance (see Table 2). Our findings are in line with the insights of several published works done on terrestrial plants, reclaimed that non-random species segregation is the rule for terrestrial plants [18, 56, 32]. A similar pattern also has been documented for threatened vascular plants [57, 58].

We observed non-random species segregation also in the matured secondary forest. It has been documented that interspecific competition for resources for light water and mineral resources could drive non-random co-occurrence patterns of species [23, 59, 60, 61, 62]. Different factors such as availability of large forest gaps from natural disturbances (e.g., fire, storms, etc.) and continuation of silvicultural treatments for better tree growth have historically supported the presence of new cohorts of vascular plants in the matured secondary forest [46]. The above-mentioned factors have a strong influence on light and mineral nutrients available in this type of forest [63] and interspecies competition for these resources could be critical reasons behind non-random species segregation.

While the entire vascular plants' community exhibits non-random co-occurrence patterns, the threatened plants alone show randomness in the managed mixed plantation forest. This forest has been managed mainly for wood production and most of the planted species are exotics (e.g. *Acacia auriculiformis*, *Acacia mangium*, *Tectona grandis*). Interestingly, most of the threatened plants of this forest stand have been originated from seeds dispersed from the adjacent natural and secondary forests and these are all native plants [45]. The strength of exotic species in exploiting available resources over native species is well entrenched in ecology [64, 65, 66]. Thus, competition between the planted exotics and native threatened species could be the reason for non-random co-occurrence patterns in the entire community while random patterns in the threatened species could be the result of seed dispersal limitation.

In the disturbed natural forest, both the entire community and the threatened assemblages within it exhibit random co-occurrence patterns. This forest has been severely disturbed by illegal removal of trees, hunting, and collection of minor forest products over hundred years, where removal of merchantable timber by the poachers is the predominant disturbance feature [46, 48]. Several studies [67, 68, 42, 29] concluded that natural

disturbances (mainly fire disturbance) are most reliable for random co-occurrence patterns in disturbed communities. However, in our study, we see that anthropogenic disturbances could also result in random co-occurrence patterns in tropical plant communities. This understanding supports the prediction that due to extensive disturbances the existing community may lose their natural harmony of co-existing via facilitation and competition [69, 70].

At the forest landscape level, our results indicate that interspecies competition could be the most critical ecological process which structures the overall vascular plant communities and the threatened plants' assemblages. Similar results are also reported in Adam [17] although Zhang et al. [19] while working on the old-growth temperate forest of China, observed random patterns on a large spatial scale. However, apart from the competition, other processes can also produce less co-occurrence among vascular plant species [71, 18]. Ecological drift or stochastic processes can produce a similar pattern those produced by competition [15, 16, 17]. Moreover, tropical plant species can co-occur infrequently due to mutual exclusiveness as a result of habitat heterogeneity and long-lasting effect of history of biogeography [72, 18]. Though null models are extensively in use in ecology to test the co-occurrence patterns, however, these are not indicative to any underlining processes that are responsible for forming communities

Assembly rules tested by the statistical null model are only a way to predict the community structure, not necessarily any direct evidence toward the processes. Only via laboratory experiments, exploring the effect of completion in structuring ecological communities is possible [71, 73]. However, several studies (see [71, 19] have attempted to control the effects of confounding factors by taking species data from homogeneous samples. Similarly, our study areas belong to a single bio-ecological zone in northeaster Bangladesh having homogeneous landforms [45]. Moreover, soil and climate maps show that like other tropical forests, our studied forests fall under a uniform temperature and precipitation regime [74, 48]. However, we could not ignore the subtle differences in environmental conditions that might influence the distributional pattern of the common vascular plants and also the threatened plants. Thus, further researches are required to explore the links among species co-occurrence patterns and biotic and abiotic heterogeneity and historical factors.

Bell [15] and Ulrich et al. [75] argued that the neutral model could generate non-random co-occurrence patterns predicted by Diamond's assembly rules model [23]. In addition, Hubble in his unified neutral theory of biodiversity, argued that only dispersal mechanisms of plant explain the biodiversity pattern of vegetation in a given forest [4]. We observed that the threatened species in our study areas exhibit very high dispersal quality.

Thus, future work must clarify the role of dispersal related process in structuring threatened communities.

5. Conclusion

Our results from null model analyses comply with the basic predictions of Diamond's assembly rules in threatened vascular plants assemblages of undisturbed natural and matured secondary forests, and at the forest landscape level [23]. But nevertheless, threatened vascular plants assemblages of the disturbed natural forest and managed mixed plantation forest follow random co-occurrence patterns and hence do not comply with Diamond's assembly rules [23]. Finally, we can reach to the conclusion that the non-random assemblage patterns are functional in the tropical plant communities. Although anthropogenic disturbances and forest management practices have strong influences upon species distribution in the tropics. However, these are not the only processes involved.

References

- [1] Clements, F.E., (1916) Plant Succession: Analysis of the Development of Vegetation. Carnegie Institution of Washington Publication Sciences, 242, 1-512.
- [2] Phillips, J.F.V. Forest succession and ecology in the Knysna area. *Memoirs of the botanical survey of south Africa*, 1931, 14: 1-327.
- [3] Gleason, H.A., The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*. 1926, 53; 7–26.
- [4] Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.
- [5] Echevarría G., Rodríguez J.P., 2017, Co-occurrence patterns of fish species in two aquatic habitats of the Arauca River floodplain, Venezuela. *Community Ecology*. 2017, 18, 137–148
- [6] Götzenberger, L., de-Bello, F., Brathen, K. A., Davison, J. et al. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews*. 2011. 9-12.
- [7] Grime, J.P., Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*. 2006, 17; 255–260.
- [8] Hillebrand, H., Matthiessen, B., Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecological Letters*. 2009, 12; 1405–1419.
- [9] Keddy, P.A., Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*. 1992, 3; 157–165.
- [10] Pitzalis, M., Montalto, F., Amore V., Luiselli L., Bologna M. A. The effects of biome and spatial scale on the Co-occurrence patterns of a group of Namibian beetles. *Acta Oecologica*, 2017, 83; 29-37.
- [11] Ricklefs, R.E., Disintegration of the ecological community. *The American Naturalist*. 2008, 172; 741–750.
- [12] Rynkiewicz, E.C., Fenton, A., Pedersen A. Linking community assembly and structure across scales in a wild mouse parasite community, *Ecology and Evolution*, 2019, 24; 13752-13763.
- [13] Scott N., Neutral Theory: A New, Unified Model for Ecology. *BioScience*, 2003, 53(2); 124–129.
- [14] Ulrich W., Gotelli N.J., Null model analysis of species associations using abundance data. *Ecology*. 2010, 91(11); 3384–3397
- [15] Bell, G., The co-distribution of species in relation to the neutral theory of community ecology. *Ecology*. 2005, 86; 1757–1770.
- [16] Ulrich, W., Species co-occurrences and neutral models: reassessing J. M. Diamond's assembly rules. *Oikos*. 2004, 107; 603–609.
- [17] Adams, D.C., Organization of Plethodon salamander communities: guild-based community assembly. *Ecology*. 2007, 88; 1292–1299.
- [18] Gotelli, N.J., McCabe, D.J., Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology*. 2002, 83; 2091–2098.
- [19] Zhang, J., Hao, Z., Song, B. et al., Fine-scale species co-occurrence patterns in an old-growth temperate forest. *Forest Management*. 2009. 257; 2115-2120.

Other processes like habitat heterogeneity, dispersal, and evolutionary history need to be considered in determining to what extent these processes reinforce or weaken threatened species co-occurrence patterns.

Acknowledgements

We wish to thank Sanjay Saha Sonet to help us during the fieldwork and Dr. Md. Mohasinul Haque for helpful comments on the manuscript. We sincerely thank Dr. Eric G. Lamb (Department of Plant Sciences, University of Saskatchewan, Canada) and his other research group members especially Christiane Catellier, Jenalee Mischkolz and Candace Piper for their constructive comments on the manuscript. We address special thanks to Professor Dr. Jasmin Joshi (Potsdam University, Germany) for her insightful comments on the scientific expression of the manuscript and for English editing. This work was co-financed by Rufford Small Grant (ID: 11191-1), UK.

- [20] Bell, G., Neutral macroecology. *Science*. 2001, 293; 2413 – 2418.
- [21] Schoener, T.W., Adler, G.H., Greater resolution of distributional complementarities by controlling for habitat affinities: a study with Bahama lizards and birds. *The American Naturalist*. 1991,137; 669–692.
- [22] Stone, L., Roberts, A., The checkerboard score and species distributions. *Oecologia*. 1990, 85; 74-79.
- [23] Diamond, J.M., Assembly of species communities. In: Cody, M.L., Diamond, J.M. (eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, 1975, pp. 342-444.
- [24] Connor, E.F., Simberloff, D., The Assembly of Species Communities: Chance or Competition? *Ecology*. 1979, 60; 1132-1140.
- [25] Gotelli, N.J., Graves, G., 1996. *Null Models in Ecology*. The Smithsonian Institution, Washington and London, pp. 153–205.
- [26] Wiens, J.A., 1989. *The ecology of bird communities*. vol. 1. Foundations and patterns. Cambridge University Press, Cambridge, UK.
- [27] Veech, J.A., A probability-based analysis of temporal and spatial co-occurrence in grassland birds. *Journal of Biogeography*. 2006, 33; 2145-2153.
- [28] Wang, Y., Chen S., Ding. P., Testing multiple assembly rule models in avian communities on islands of an inundated lake, Zhejiang Province, China. *J. Biogeogr*. 2011, 38; 1330-1344.
- [29] Sanders, N.J., Gotelli, N.J., Wittman, S.E. et al., Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography*. 2007, 34; 1632–1641.
- [30] Cardillo, M., Meijaard, E., Phylogeny and co-occurrence of mammal species on Southeast Asian islands. *Global Ecology and Biogeography*. 2010, 19; 465–474.
- [31] Ulrich, W., Zalewski, M., Hajdamowicz, I. et al., Tourism disassembles patterns of co-ence and weakens responses to environmental conditions of spider communities on small lake islands. *Community Ecology*. 2010, 11; 5-12.
- [32] Maltez-Mouro, S., Maestre, F.T., Freita, H. Co-occurrence patterns and abiotic stress in sand-dune communities: Their relationship varies with spatial scale and the stress estimator. *Acta Oecologica*. 2010, 36; 80–84.
- [33] Callaway, R.M., 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.
- [34] Keddy, P.A., 2001. *Competition*, second ed. Kluwer, Dordrecht.
- [35] Conservation International. 2018. *Biodiversity Hotspots*, Available in: <http://www.biodiversityhotspots.org/xp/hotspots> (Accessed 10 October 2018)
- [36] Slik, J.W., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C. et al. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*. 2013,22, 1261–1271.
- [37] Wright, S.J., The future of tropical forests. *Annals of the New York Academy of Sciences*. 2010, 1195: 1–27.
- [38] Clark, D.A., Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. *Biotropica*. 2007, 39; 4–19.
- [39] Comita, L.S., Thompson, J., Uriarte, M., Jonckheere, I. et al., Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. *Ecological application*. 2010, 20; 1270–1284.
- [40] Brockerhoff, E.G., Hervé, J., Parrotta, J.A. et al. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation*. 2008. 17(5); 925-951.
- [41] Norden, N., Chazdon, R.L., Chao, A. et al., Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecological Letters*. 2009, 12; 385-394.
- [42] Silva, I.A., Carvalho, G.H., Loiola, P.P., Herbaceous and shrubby species co-occurrences in Brazilian savannas: the roles of fire and chance. *Community Ecology*. 2010, 11; 97-104.
- [43] BCAS (Bangladesh Centre for Advanced Studies)., 1997. *Final Report. Prep'For Forest Resources Management Project*. Biological Survey. Forest Department, Dhaka.
- [44] Sarker, S.K., Sonet, S.S., Haque, M.M. et al., Disentangling the role of soil in structuring tropical tree communities at Tarap Hill Reserve of Bangladesh. *Ecological Research*. 2013, 28; 553-565.
- [45] IUCN. 2004. *Flora of Rema Kalenga wildlife sanctuary*. IUCN Bangladesh Country office Dhaka. pp. 122.
- [46] Uddin, M.Z., Hassan, M.A., 2011. *Plant Genetic resources of Rema-Kalenga Wildlife Sanctuary, Bangladesh*. LAP LAMBERT Academic Publishing, Germany.
- [47] Canonizado, J.A., Rahman. S.M., 1988. *GOB/WB Forest resource management project technical assistance component: integrated forest management plan for the Sylhet forest division*. Mandala Agricultural Department Corporation and Forest Department, Ministry of Environmental and Forest, Dhaka, Bangladesh, pp 1-4.
- [48] NACOM (Nature Conservation Management), 2003. *Secondary Data Collection for Pilot Protected Areas: Rema-Kalenga Wildlife Sanctuary*. Ministry of Environment and Forest, Bangladesh, pp. 1-23.

- [49] Siddiqui, K.U., Islam, M.A., Ahmed, Z.U. et al., (Eds) 2007. Encyclopedia of Flora and Fauna of Bangladesh, Vol. 11. Angiosperms; Monocotyledons. Asiatic Society of Bangladesh, Dhaka.
- [50] Bangladesh National Herbarium., 2001. Red data book of vascular plants of Bangladesh. Bangladesh National Herbarium, Dhaka.
- [51] Gotelli, N.J., Null model analysis of species co-occurrence patterns. *Ecology*. 2000, 81; 2606–2621.
- [52] Gotelli, N.J., Ellison. A.M., Assembly rules for New England ant assemblages. *Oikos*. 2002, 99; 591-599.
- [53] Manly, B.F.J., A note on the analysis of species co-occurrences. *Ecology*. 1995, 76; 1109-1115.
- [54] Gotelli, N.J., Entsminger, G.L., 2006. EcoSim: null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear. <http://garyentsminger.com/ecosim.htm>.
- [55] IUCN. 2017. The IUCN red list of threatened species. Available in: <http://www.iucnredlist.org/> (Accessed 20 January 2017).
- [56] Hao, Z.Q., Zhang, J., Song, B. et al., Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. *Forest Ecology and Management*. 2007, 252; 1–11.
- [57] Gjerde, I., Saetersdal, M., Blom, H., Complementary hotspot Inventory- A method for identification of important areas for biodiversity at the forest stand level. *Conservation Biology*. 2007, 137; 549-557.
- [58] Gjerde, I., Saetersdal, M., Rolstad, J. et al., Fine-Scale Diversity and Rarity Hotspots in Northern Forests. *Conservation Biology*. 2004,18; 1032–1042.
- [59] Hanski, I., Spatial pattern of co-existence of competing species in patchy habitat. *Theoretical Ecology*. 2008, 1; 29-43.
- [60] Kelt, D.A., Brown, J.H., Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In: Weiher, E., Keddy, P.A. (eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, 1999, pp. 75–107.
- [61] Kemp, J.E., Bergh, N.G., Soares, M., Ellis, A.G., Dominant pollinators drive non-random community assembly and shared flower colour patterns in daisy communities. *Annals of Botany*, 2018, 123;277–288.
- [62] Tilman, D., Interspecific competition and multispecies coexistence. In: May, R., McLean A. (eds.), *Theoretical Ecology: Principles and Applications*. 3rd edn. Oxford University Press, New York, 2007. pp. 84–97.
- [63] Latham, P.A., Zuuring, H.R., Coble, D.W., A method for quantifying vertical forest structure. *Forest Ecological Management*. 1998, 104; 157–170.
- [64] Fajardo, A., Gundale, M.J., Canopy cover type, and not fine-scale resource availability, explains native and exotic species richness in a landscape affected by anthropogenic fires and posterior land-use change. *Biological Invasions*. 2018, 20; 385-398.
- [65] Strauss, S.Y., Lau J.A., Carroll. S.P., Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecological Letters*. 2006, 9; 357–374.
- [66] Thomas Bøhn, T., Amundsen, P., Sparrow, A., Competitive exclusion after invasion? *Biological Invasion*. 2008, 10; 359–364.
- [67] Gotelli, N.J., Arnett, A.E., Biogeographic effects of red fire ant invasion. *Ecological Letters*. 2000, 3; 257–261.
- [68] Sara, M., Bellia, E., Milazzo, A., Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands. *Journal of Biogeography*. 2006, 33; 843–852.
- [69] Schamp, B.S., Aarssen, L.W., The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos*. 2009, 118; 564 -572.
- [70] Weiher, E., Keddy, P.A., Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*. 1995, 74; 159-164.
- [71] Burns, K.C., Patterns in the assembly of an island plant community. *Journal of Biogeography*. 2007, 34; 760-768.
- [72] Cracraft, J., Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. *Systemic Zoology*. 1988, 37; 221–236.
- [73] Von-Holle, B., Simberloff, D., Testing Fox's assembly rule: does plant invasion depend on recipient community structure? *Oikos*. 2004, 105; 551–563.
- [74] Chave, J., 2008. Spatial variation in tree species composition across tropical forests: pattern and process. In: Carson, W.P. and S.A. Schnitzer (eds.), *Tropical forest community ecology*. Wiley/Blackwell, West Sussex. pp. 11–30.
- [75] Ulrich W., Jabot, F., Gotelli, N. J., Competitive interactions change the pattern of species co-occurrences under neutral dispersal. *Oikos*. 2017,91-100.