Changes in Community Composition of Tropical Evergreen Forests during Succession in Ta Dung National Park, Central Highlands of Vietnam

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Abstract: Degradation of tropical forests is a major driver of the global extinction crisis. A key question is understanding the role of evolution history during forest succession in the context of forest restoration for maintaining ecosystem function and stability. This study was conducted in a fragmented forest landscape in the central highlands of Vietnam. We sampled living trees with diameters at breast height of ≥6.0 cm in nineteen 0.25 ha plots to evaluate forest community structure changes over two early successional stages (<10 years and 10–20 years old) after abandonment and old-growth. We used both statistically metric and nonmetric analyses to examine correlations of community composition during successional stages and along elevational gradients. We found that (i) significant differences existed in the structural compositions between early successional forests and old-growth forests, but did not exist within early successional forests; (ii) the phylogenetic structure shifted from overdispersion to clustering with increasing successional ages; and (iii) above-ground biomass (AGB), representing ecosystem functioning, significantly increased from early-to-late successional stages, but did not correlate with phylogenetic diversity or elevation. Our results revealed that the forest community structure was strongly affected by degradation, particularly AGB and phylogenetic structure. These findings have clear implications for sustaining biodiversity persistence and ecosystem functioning in human-modified landscapes in the study region.

Keywords: above-ground biomass; biodiversity; phylogenetic diversity; community assembly; tropical rain forest

1. Introduction

Degraded tropical forests due to anthropogenic disturbance are rapidly expanding in the tropics at alarming rates [1,2]. The conversion of tropical forest to monocultural plantations and agricultural

lands led to mosaic landscapes with various spatial arrangements of tropical evergreen forests of widely varying ages [3]. Considering that forest resilience in maintaining its function and structure is associated with history, evolutionary pressures, and previous extinction, conservation actions should target entire communities, rather than species [4]. Previous studies on forest succession focused on changes in phylogenetic structure and dispersion during succession [3,5–7], while the ecological theory assumes that diversity is positively correlated with productivity when diversity increases niche complementarity, for example, complementary resource use [8]. Few studies quantified the relationship between biodiversity and ecosystem functions (e.g., phylogenetic diversity and forest productivity) during successional process in tropical forests [3,6,8]. Expectedly, this approach allows scientists to better understand community assembly by considering the long-term evolutionary history of coexisting species [9].

Phylogenetic diversity is assumed to be a good predictor of community stability in biomass productivity throughout space and time as it contains more information about species complementarity, in which a more diverse plant community is able to use resources more completely, thereby, increasing productivity [10–13]. In the tropical forests of Costa Rica, Lasky et al. [8] found a strong correlation between phylogenetic diversity and above-ground biomass (AGB) during the early stages of forest succession. Across geographical regions in the United States, Potter and Woodall [14] reported that phylogenetic diversity was significantly associated with AGB, but weakened with both increasing site productivity and live tree stocking. However, in a subtropical forest of South China, Ouyang et al. [6] found no significant effect of species and phylogenetic diversity on forest biomass in any phase (early, mid, or late) of forest succession. In addition, Rozendaal and Chazdon [15] stated that, depending on the interactions between tree mortality and growth, biomass dynamics were largely regulated by tree growth in early succession and by both in later succession.

The relationship between phylogenetic diversity and forest ecosystem function is simultaneously influenced by many factors, such as disturbance, edaphic and topographic heterogeneity, and speciation [6,16–18]. Phylogenetic clustering suggests abiotic factors drive community assembly processes leading more closely related species to coexist, which in turn, tend to share similar niches, phenotypes in a particular environment, and sensitivities to disturbance [19,20]. Phylogenetic overdispersion, on the other hand, is assumed to dominate later successional stages because of competitive exclusion governing species establishment [3,21,22] as a result of biotic processes, such as species interaction, dispersal and speciation.

Habitat filtering (sunlight, temperature, soil types, topography) plays an important role in selecting species during colonization [3,21]. In addition, Mi et al. [23] found a dominance of stochastic processes with significant interactions between the environment and disturbance over succession, concluding that post-disturbance restoration may be largely unpredictable and difficult to control in subtropical forests. Among abiotic factors, elevation is assumed to have a significant impact on the vegetation structure of most mountain ranges in the world, particularly species diversity, which varies largely depending on the interaction between plant communities, species, and environmental factors [24]. In the tropical forests of Southeast Asia, Satdichanh et al. [3] found a strong correlation between soil fertility and community structure in the early successional stages, with significant elevation associated with above-ground biomass only in forests younger than 100 years. In the mountainous region of Veracruz, up to 3500 m a.s.l, Mexico, Monge-González et al. [25] found a correlation between tree diversity and community composition along elevational gradients of disturbed forests.

To better understand the change in forest biodiversity and ecosystem functioning, over time, herein, we study the relationship between evolutionary history (phylogenetic diversity and community structure) and forest productivity (e.g., volume and above ground biomass) through different successional forest phases in a mosaic landscape in the central highlands of Vietnam (Figure 1). The present paper uses data from 19 plots from tropical evergreen forests covering three successional stages (early, early–mid, and old-growth), addressing the following questions: (1) How do community structure and phylogenetic diversity change over different successional forest phases? and (2) Do

taxonomic and phylogenetic diversity correlate with forest productivity and elevation during forest succession?
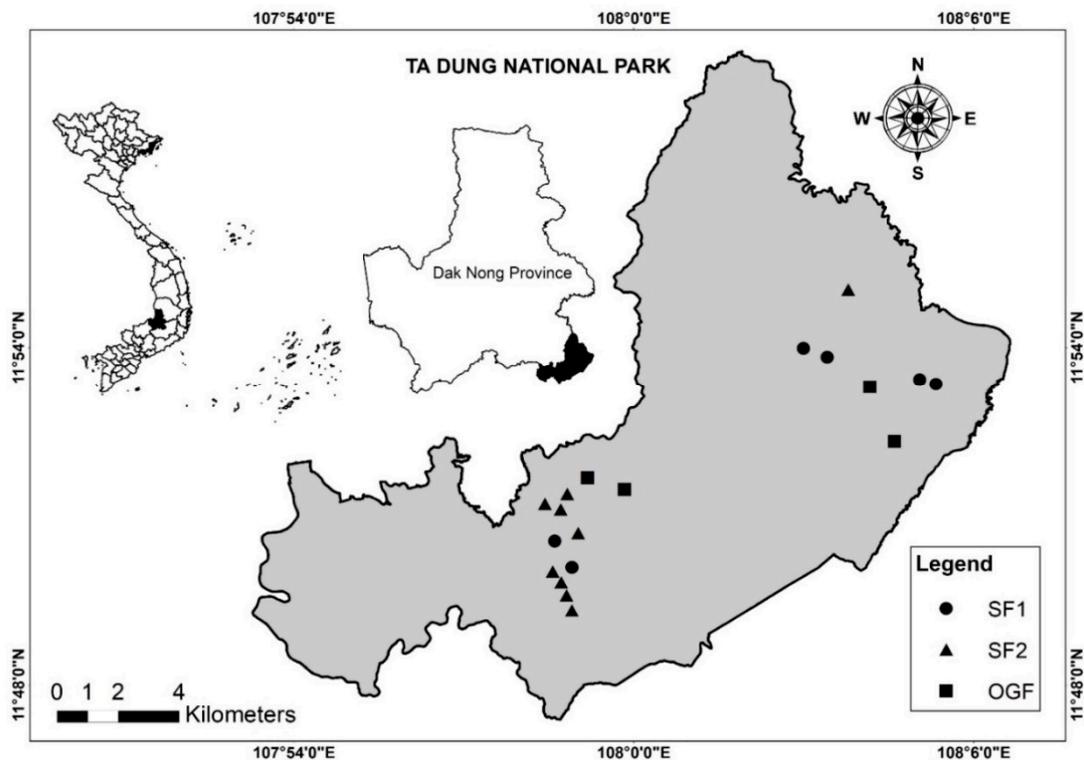
Figure 1. Map of Ta Dung National Park and study plots. Circles are secondary forest plots <10 years old (SF1), triangles are secondary forest plots 10–20 years old (SF2), and squares are old-growth forest plots (OGF).

2. Materials and Methods

2.1. Study Site and Data Collection

The study was conducted at Ta Dung National Park, located in the central highlands of Vietnam (Figure 1). In 2013, The National Park was established in order to maintain high forest protection from human disturbance. Before that time, this region was disturbed by local people in easy access areas, for example, areas close to main roads, local villages, or areas at low elevation, for timber collection or crop plantation. The climate is strongly affected by the seasonal climate, with about 90% of total precipitation falling from April to November and the dry season lasting from December to March. The average annual rainfall is about 2513 mm and the annual mean humidity is 84%. The mean annual temperature is 22.5 °C, while the lowest temperature is 14 °C in December and the highest temperature is 35 °C in April.

In this study, we classified forest successional stages according to plot land use and disturbance history. The successional stages used were according to secondary forest since abandonment; (a) <10 years old (SF1, early); and (b) 10–20 years old (SF2, early–mid), recovering after illegal logging or slash-and-burn for annual crop plantation, thereby lacking large-diameter trees; and (c) old-growth forest (OGF), a primary forest with tall, large-diameter trees without visible signs of recent human disturbance. The successional stage was assigned at the plot level with help by staff from the National Park.

During 2019–2020, we established 19 plots of 0.25 ha (50 × 50 m) each, including six plots in SF1, nine plots in SF2, and four plots in OGF. All live trees with diameters at breast height (dbh) of ≥6.0 cm were recorded in terms of their characteristics (species, dbh, and total tree height). The location and elevation of each study plot were recorded using the GPS Garmin 60s (Garmin Coporation, Taiwan).

2.2. Data Analysis

2.2.1. Community Diversity and Structure

Above-ground biomass (AGB) was estimated according to the allometric equation obtained by Chave et al. [26] for pantropical forest stands as,

$$AGB = 0.0673 \times (D^2 \times H \times \rho)^{0.976} \tag{1}$$

where D is dbh (cm), H is total height (m), and ρ is the wood-specific density (g/cm^3). We obtained the wood-specific density ρ for the observed species/genera from various sources [27–31]. In cases where a range of wood density values were reported, we used a median value. Where wood density data were unavailable for a species, the average across all species in that genus or mean wood-specific density of that plot was applied (see [32]).

We used five commonly used and ecologically interpretable indices of taxonomic diversity emphasizing different aspects of species diversity [33], namely, species richness (SR), the Shannon's H and Simpson's D indices of entropy, Margalef's richness (Ma), and Fisher's alpha (Fa). Species richness is the number of species found in a plot. Simpson's dominance is weighted toward the abundance of a species combining species richness and evenness. The Shannon index is more sensitive to rarer species, while the Simpson index [34] responds more to abundant species, both representing two points in a spectrum of relative sensitivity to species number versus relative evenness [35]. Fisher's alpha index was calculated for all trees within each plot [36], combining species richness and abundance in a single metric that is relatively independent of sample size and is commonly used in studies of tropical tree diversity (e.g., [37]). Margalef's richness was calculated, including the number of species and the total amount of individuals in a sample [38].

Species diversity indices were calculated separately for each plot in each forest type using the software PAST ver. 3.25 (PAleontological Statistics, https://folk.uio.no/ohammer/past/). The data of the 19 plots were pooled to model the dbh height curves for all tree individuals, which were fitted best using the equation of Prodan [39].

2.2.2. Phylogenetic Diversity and Structure

We used a phylogenetic mega-tree approach to construct separate family level phylogenetic trees to study forest communities. All tree species names were standardized following taxonomic name resolution service ver. 4.0 [40] at http://tnrs.iplantcollaborative.org. We then assembled species lists into phylogenies using the phylomatic and the maximum resolved super-tree of Angiosperm Phylogeny Group (APG) IV (R20160415.new, [41]) at http://phylodiversity.net/phylomatic/. To evaluate the phylogenetic structure of tree communities, we used the phylogenetic metrics mean phylogenetic distance (MPD), net related index (NRI), net nearest taxon index (NTI), and mean nearest taxon distance (MNTD) [42], which were calculated using Phylocom software ver. 4.2 [43].

NRI analyzes the degree of phylogenetic relatedness by measuring mean pair-wise phylogenetic distances among constituent species in a community relative to that found in the species pool. Therefore, NRI analyzes phylogenetic structure throughout the phylogeny, while NTI only reflects phylogenetic clumping at the terminal tips of a phylogeny. Using the Phylocom software, the branch lengths of the phylogenies were calibrated using the function Bladj and the node ages were provided by [44], while alpha MPD and NRI were calculated through the function Comstruct by using the "-a" argument to weight species by their abundance. To calculate NRI, we firstly compared the observed values of MPD with those obtained by chance after generating 999 communities from the null model, which maintained the species richness of each sample and randomized species occurrence [45]. NRI and NTI were calculated as following,

$$NRI = -\left(\frac{MPD_{obs}-MPD_{rd}}{sdMPD_{rd}}\right) NTI = -\left(\frac{MNTD_{obs}-MNTD_{rd}}{sdMNTD_{rd}}\right) \tag{2}$$

where MPD$_{obs}$ is the observed mean phylogenetic distance, MPD$_{rd}$ is the expected mean phylogenetic distance of randomized species assemblages, sdMPD$_{rd}$ is the standard deviation of the mean phylogenetic distance of randomized species assemblages, MNTD$_{obs}$ is the observed mean nearest taxon distance, MNTD$_{rd}$ is the expected mean nearest taxon distance of randomized species assemblages, and sdMNTD$_{rd}$ is the standard deviation of the mean nearest taxon distance of randomized species assemblages.

Positive NRI and NTI values indicate phylogenetic clustering (i.e., species are more closely related than expected by chance) while negative values indicate phylogenetic overdispersion (i.e., species are more distantly related than expected by chance) [45]. Using Phylocom 4.2, we measured Faith's PD, the sum of branch lengths of the subtending tree of the species present in a community [46], which does not account for species abundance, and Rao's quadratic entropy index Dp, an extension of the Simpson diversity index that incorporates the phylogenetic distance between each pair of species [47].

2.2.3. Correlation between Community Diversity and Structure

We examined changes in tree community composition among forest successional stages, such as the stand characteristics (including the number of tree individuals (N) and AGB), species diversity (containing H, 1-D, Ma, and Fa) and phylogenetic structure (including SR, NRI, NTI, MPD, PD, Dp, and MNTD) using the following methods:

(1)　Non-metric multidimensional scaling (NMDS) with abundance-based Bray–Curtis dissimilarities (adjustment noshare = 0.1; 999 permutations) was used to test the differences in tree community composition using a nested permutational multivariate analysis of variance (PERMANOVA, 999 permutations). All statistical analyses were performed in R ver. 3.5.1. All tests and ordination plots were computed using the package vegan ver. 2.4–5 [48]. The variables were fitted onto the NMDS ordinations using the envfit function in the vegan package and goodness of fit and *p*-value were computed 999 times, in order to detect environmental drivers for community dynamics.

(2)　Data normality and homogeneity of variances were tested using one-way ANOVA with the Shapiro–Wilk and Levene tests. When the ANOVA indicated a significant difference among forest categories ($p < 0.05$, F test), the differences between means were tested with Scheffe post-hoc test. All statistical analyses were performed using STATISTICA 9.1 (StatSoft, Inc., Tulsa, OK, USA).

3. Results

3.1. Plant Community

A total of 1198 (199.00 ± 54.38) individual trees belonging to 103 species, 79 genera, and 40 families were recorded in six early successional forest plots, less than 10 years old of succession (Table 1). At nine early–mid successional forest plots 10–20 years old of succession, 2468 (274.22 ± 76.53) individual trees of 119 species, 88 genera, and 46 families were measured (Appendix A Table A2). At four old-growth forest plots, a total of 1048 (262.0 ± 30.61) individuals were counted, belonging to 90 species, 72 genera, and 41 families.

The DBH–height relationship of the three restoration time forest types was well fitted by Prodan (1951), with R^2 ranging from 0.52 to 0.76 the strongest correlation at OGF (Figure 2). It was observed that the height curve along a DBH gradient is superior in OGF (Figure 2c) compared to SF1 and SF2 (Figure 2a,b), for a certain DBH value, with the height increment greater than those observed in SF1 and SF2 (Figure 2d).

Table 1. Structural characteristics and species diversity of the three forest types, (Mean ± SD).

Structural Properties	SF1	SF2	OGF
Stand structure			
Density of trees	199.00 ± 54.38 a	274.22 ± 76.53 a	262.00 ± 30.61 a
Basal area (m^2)	2.24 ± 1.05 a	4.29 ± 2.00 a	9.49 ± 1.46 b
Volume (m^3)	8.92 ± 5.26 a	21.16 ± 12.79 a	80.55 ± 16.99 b
AGB (Mg)	8.24 ± 4.71 a	21.37 ± 13.53 a	76.88 ± 15.82 b
Species diversity			
Species richness	35.00 ± 8.07 a	41.78 ± 10.21 ab	52.75 ± 1.71 b
Shannon's index	2.77 ± 0.51 a	2.84 ± 0.52 ab	3.46 ± 0.01 b
Margalef's index	6.47 ± 1.47 a	7.28 ± 1.64 ab	9.31 ± 0.46 b
Fisher's alpha	12.95 ± 4.26 a	14.04 ± 4.35 ab	20.08 ± 2.21 b
Simpson's index	0.87 ± 0.11 a	0.86 ± 0.15 a	0.95 ± 0.01 a

Values for a parameter followed by different letters differ significantly ($p < 0.05$).
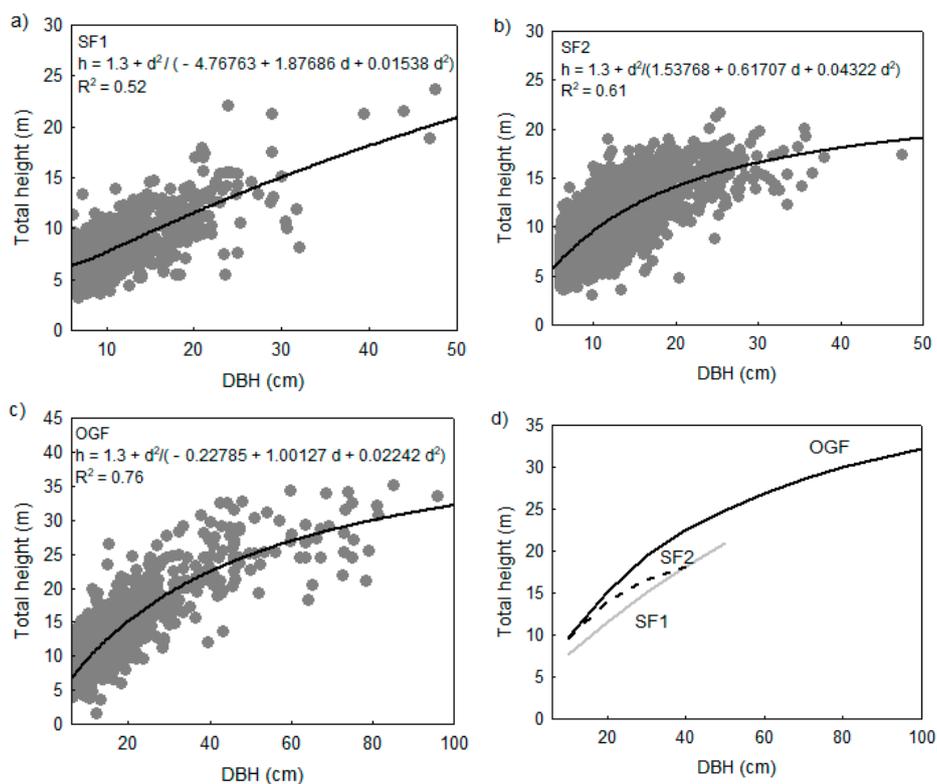
Figure 2. DBH–total height relationship of trees in three forest types.

3.2. Compositional Pattern of Forest Community

Significant differences were found between the structural compositions of the forest types, particularly between secondary forests (SF1 and SF2) and old-growth forest (OGF). The PERMANOVA analysis showed statistical significance in the community structure of the three forest types (F = 2.4651; R^2 = 0.23555, p = 0.0011). However, no significance difference was found in the community structure between the secondary forests SF1 and SF2 (F = 1.0851, R^2 = 0.07704; p = 0.3219).

Fitting the structural community variables with elevation to the NMDS plot, the results showed a significant correlation with p-values of <0.05 (detail in Appendix A Table A1.), including community diversity and functioning (SR with R^2 = 0.44, H with R^2 = 0.33, 1-D with R^2 = 0.5, Fa with R^2 = 0.4 and AGB with R^2 = 0.69), phylogenetic structure (MNTD with R^2 = 0.52, NTI with R^2 = 0.63, Dp with R^2 = 0.58), and El with R^2 = 0.66) (in red in Figure 3), while N, MPD, NRI, and PD had no correlation, with p-values of >0.05 (in black in Figure 3).
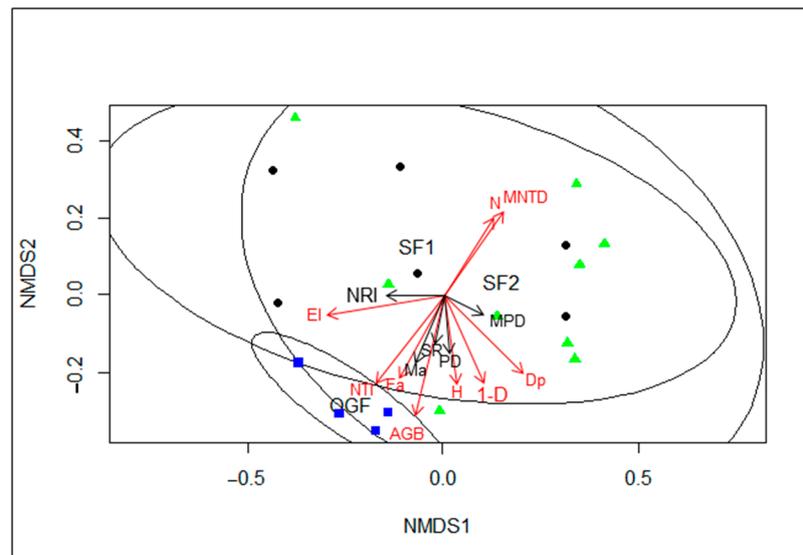
Figure 3. NMDS ordination showing dissimilarities of the compositional structure of the forest types in ellipses: OGF: Old-growth forests (blue squares); SF1:-secondary forests (green triangles); SF2:-secondary forests (black circles) with stress value = 0.09. Significant variables ($p < 0.05$) are displayed in red arrows and nonsignificant variables ($p > 0.05$) in black arrows. N: number of individuals, SR: species richness; H: Shannon, (1-D): Simpson, Ma: Margalef, and Fa: Fisher indices; MPD: mean phylogenetic distance, NRI: net related index, NTI: net nearest taxon index, MNTD:-mean nearest taxon distance, PD: phylogenetic diversity; AGB: above-ground biomass, El: elevation.

3.3. Correlation of Community Composition

Tree density per plot did not differ significantly among the three restoration type forests (199 individuals per ha in SF1, 274 in SF2 and 262 in OGF) (Table 1). However, in OGF, basal area (9.49 ± 1.46, m^2), volume (80.55 ± 16.99, m^3), and AGB (76.88 ± 15.82, Mg) per plot were significantly greater than in the other two forest types (Table 1), but these structural properties did not differ between SF1 (2.24 ± 1.05 m^2; 8.92 ± 5.26 m^3; 8.24 ± 4.71 Mg) and SF2 (4.29 ± 2.00 m^2; 21.16 ± 12.79 m^3; 21.37 ± 13.53 Mg).

Species richness (number of species) per plot was significantly lower in SF1 (35.00 ± 8.07) and SF2 (41.78 ± 10.21) than in OGF (52.75 ± 1.71) ($p < 0.05$, Scheffe post-hoc test, Table 1), but no significant differences were found between SF1 and SF2 ($p > 0.05$, Scheffe post-hoc test). The same pattern was detected also for other diversity indices; Shannon, Margalef, and Fisher alpha indices were significantly greater in OGF compared to the two successional forests (SF1 and SF2), and no significant differences between them were tested. Simpson's index did not differ among forests ($p > 0.05$, Scheffe post-hoc test).

MPD showed the highest value in SF1 (25.17 ± 0.90) and the lowest in OGF (21.85 ± 0.63), with significant differences between them (Table 2, details in Appendix A, Figures A1–A3). NRI values were positive in all OGF communities, indicating a clustered phylogenetic structure, but the NRI values of two of six plots (approximately 33%) in SF1 and four of nine plots (approximately 44%) in SF2 were negative, indicating phylogenetic over-dispersion. NRI were greater in OGF (1.44 ± 0.48) than SF1 (0.502 ± 0.91) and SF2 (0.02 ± 0.98) but differed in SF2. NTI values were positive in all OGF cases, three cases (approximately 50%) in SF1, and six cases (approximately 66%) in SF2, indicating phylogenetic clustering. NTI values were greater significantly in OGF (1.75 ± 0.61) than in SF1 (0.29 ± 0.82), but did not differ between SF1 and SF2 (0.07 ± 1.62). MNTD values were greater significantly in SF1 (6.64 ± 1.28) than in OGF (4.84 ± 0.53), but also did not differ between SF1 and SF2 (6.43 ± 2.09). PD and Dp indices did not differ between all three successional forest stages ($p > 0.05$).

Table 2. Phylogenetic structure and diversity of the three forest types (mean ± SD).

Plot	Elevation (m)	MPD		NRI		NTI		PD		Dp		MNTD	
SF1-Early succession													
1	1117	25.6		0.04		1.24		239		10.84		5.78	
2	1092	24.45		0.97		−0.24		200		8.97		8.13	
3	1152	25.88	25.17 ± 0.90 b	−0.33	0.502 ± 0.91 ab	1.4	0.29 ± 0.82 b	320	249.17 ± 45.78 a	11.94	10.75 ± 1.33 a	4.91	6.64 ± 1.28 b
4	1199	24.79		1.28		−0.57		289		9.29		6.05	
5	668	26.3		−0.53		−0.13		219		12.07		7.97	
6	718	23.97		1.7		0.04		228		11.4		7.03	
SF2 -Early-mid succession													
1	1300	16.23		1.3		0.81		187		8.12		5.47	
2	984	21.76		0.72		1.61		253		10.88		4.67	
3	1013	23.14		0.2		0.7		306		11.57		5.09	
4	970	24.66	22.69 ± 3.02 ab	−1.12	0.02 ± 0.98 b	0.97	0.07 ± 1.62 b	273	256.56 ± 35.85 a	12.33	11.35 ± 1.51 a	4.72	6.43 ± 2.09 ab
5	704	25.05		−0.69		1.8		280		12.53		4.53	
6	676	23.44		−0.13		0.61		223		11.72		6.33	
7	738	26.03		−1.42		−2.97		266		13.01		9.72	
8	732	23.98		0.04		−1.34		282		11.99		7.71	
9	657	19.97		1.3		−1.51		239		9.98		9.62	
OGF-Old-growth													
1	1002	22.39		1.13		1.23		287		11.19		5.29	
2	1061	22.19	21.85 ± 0.63 a	1.27	1.44 ± 0.48 a	1.39	1.75 ± 0.61 a	280	278.75 ± 6.65 a	11.09	10.92 ± 0.32 a	5.25	4.84 ± 0.53 a
3	1285	21.93		1.22		1.81		277		10.96		4.64	
4	1417	20.93		2.16		2.6		271		10.46		4.17	

MPD: mean phylogenetic distance, NRI: net related index, NTI: net nearest taxon index, PD: phylogenetic distance, Dp: Rao's quadratic entropy index, MNTD: mean nearest taxon distance. Values for a parameter followed by different letters differ significantly ($p < 0.05$).

4. Discussion

Our results showed changes in community structure and phylogenetic diversity over successional forest stages, exhibiting correlations of taxonomic and phylogenetic diversity with forest productivity and elevation. The results showed that the community structure presents changes during forest succession. There was a significant difference between the secondary forests (early and early-mid successions) and old-growth forest in structural composition and phylogeny, while no significant difference within early-successional forests. Community composition and productivity positively correlated with forest succession and elevation.

Our results showed that structural attributes, such as stem density, basal area, volume and AGB were significantly different between the secondary and old-growth forests, but were non-significantly different within the secondary forests. In our study site, AGB increased from 8.24 to 76.88 Mg/plot (ca. 32.96–307.52 Mg/ha) from secondary forest to old-growth forest types. consistent with previous studies conducted in the central highlands of Vietnam, geographically close to Ta dung National Park [27,30]. Species richness increased from 35 to 52 species from early successional to old-growth forests (Table 1). In a previous study on relationships between species richness and forest productivity, Ouyang et al. [49] found that stand density and age were more important drivers regulating total biomass than species diversity, which has a positive effect on forest productivity in the subtropical forests of China. This effect was consistent with our findings and emphasized the importance of stand density, forest age, and species diversity, whereby, increasing diversity enhances forest productivity and increasing the chance of possessing highly productive species [50,51].

Phylogenetic analyses indicated that old-growth forest contained more closely related species than expected by chance, as shown by phylogenetic clustering and confirmed by positive values of the net-related index and net-nearest taxon indices (Table 2). Moreover, the community structure shifted from overdispersion to clustering in the secondary forest of successional stages <10 years old and 10–20 years old, suggesting evidence that species assembly and colonization dominate ecological

processes, such as niche assembly or facilitation during early forest succession. Our results were contrasted by the findings by Satdichanh et al. [3], conducted in tropical forests of Southeast Asia, who found the phylogenetic community structure shifted from clustering to overdispersion with increasing successional ages from 15–30 years old in secondary forests to old-growth forest. The changes in phylogenetic plant community structure during succession may be regulated by environmental filtering or biotic interactions (deterministic factors such as species, functional, and phylogenetic turnover) or stochastic factors [3,23]. Throughout successional stages, species co-occurring within sites are functionally clustered indicates that community assembly is deterministic with respect to species traits [22]. Taxonomic and phylogenetic diversities showed no significant differences (Tables 1 and 2), indicating that these evidences mainly reflect colonization and closely related species [22], which remained during succession in our forest types. Hence, we conclude that as forest succession proceeds, species assembly possesses relative importance, rather than competitive exclusion in our study site.

Recent studies argued the relative importance of phylogenetic and taxonomic diversity in promoting ecosystem stability and community biomass productivity [12,52–55]. For instance, Yuan et al. [55] and Venail et al. [12] reported that phylogenetic diversity does not predict ecosystem functioning, for instance species richness and phylogenetic diversity, while Larkin et al. [53] agreed that phylogenetic diversity provides good information for management and restoration interventions. In this study, phylogenetic and taxonomic diversity were not significantly different between early successional ages, suggesting a failure in detecting phylogenetic diversity as a predictor for ecosystem function. Previous studies [3,11,13,56] argued that this failure may be caused by inappropriate study design when considering the species pool, experimental design, and analyses, such as using inappropriate phylogenies, skewed distributions of phylogenetic distances or the absence of sufficient niche space in experimental and observational venues [57].

Previous studies reported that forest biomass decreases with decreasing elevation [58–60]. In our study, the NMDS analyses showed that elevation significantly correlated with community attributes (e.g., species diversity and above-ground biomass) and phylogenetic structure (NTI and Dp) with *p*-values of <0.05 (Appendix A Table A1), particularly in old-growth forest. These findings were consistent with other studies conducted in Southeast Asian forests (e.g., [3,61]. In a tropical forest of Hainan Island, China, Zhu et al. [24] found a community composition, such as tree abundance, species richness, and phylogenetic diversity increased up to 700 m a.s.l and decreased at the highest elevations of 1175 m, while our results were analyzed up to elevation of 1417 m. Regionally, in Southeast Asia, Culmsee et al. [60] found opposite trends of taxonomic richness and phylogenetic diversity in Malesian mountain forests at elevations from 650 to 3080 m a.s.l.

5. Conclusions

We used a variety of techniques to understand community structure and phylogenetic diversity of trees in Ta Dung National Park, Vietnam. Our study showed variations in phylogenetic diversity and community structure, changing over successional stages of tropical species-rich forests. The results demonstrated the complexity and variability in forest succession of tropical rain forest. From young- to old-growth forests, the structural compositions differed between early successions and old-growth forests, but not within early successional forests. The phylogenetic structure shifted from overdispersion to clustering, while the above-ground biomass-AGB increased, but was not associated with phylogenetic diversity or elevation. Our results suggest that biodiversity and stand structure should be considered simultaneously to evaluate and monitor the effectiveness of management practices in order to recover disturbed forest stands. Long-term experimental and comprehensive studies considering key biotic (including community properties) and abiotic (such as elevation, aspect, and slope) factors should be carried out in order to observe the changes during forest succession for the maintenance of forest biodiversity and function.

Appendix A

Table A1. NMDS ordination of the compositional structure of three forest types.

	NMDS1	NMDS2	r^2	*Pr(>r)*
El	−0.99225	−0.12427	0.6608	0.002
N	0.50871	0.86094	0.4423	0.009
AGB	−0.32277	−0.94648	0.6935	0.001
X1.D	0.41065	−0.91179	0.5036	0.003
H	0.17959	−0.98374	0.3267	0.041
Fa	−0.45491	−0.89054	0.4011	0.018
Ma	−0.39278	−0.91963	0.2733	0.074
SR	−0.28326	−0.95904	0.1225	0.331
MPD	0.9323	−0.36169	0.0882	0.5
NRI	−0.9995	−0.03152	0.1574	0.275
NTI	−0.54346	−0.83943	0.6318	0.001
PD	0.1418	−0.9899	0.1624	0.233
Dp	0.6978	−0.71629	0.5767	0.003
MNTD	0.56364	0.82602	0.5168	0.008

NMDS1 and NMDS2: Non-metric multidimensional scaling axes, r: proportion, *Pr*: significance.

Figure A1. Phylogenetic tree of OGF.
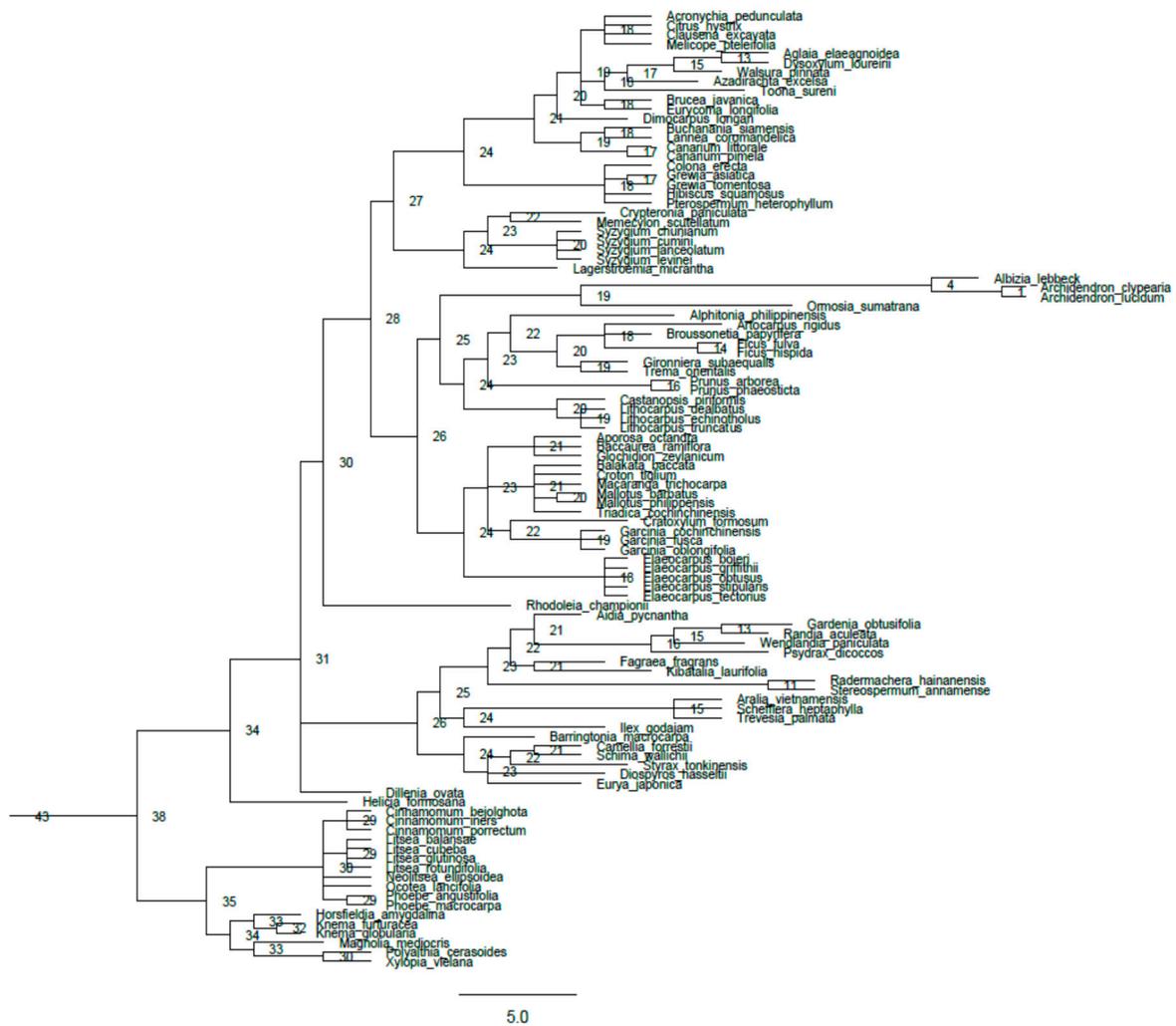
Figure A2. Phylogenetic tree of SF1.

Figure A3. Phylogenetic tree of SF2.

Table A2. Number of Species Individuals Per Study Plot.

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
1	*Acronychia pedunculata* (L.) Miq.	Rutaceae	20	2	12		1	5	1	41	62	4	6	6	4	11	3	1	2	9	7
2	*Actinodaphne pilosa* (Lour.) Merr.	Lauraceae									3											
3	*Aglaia elaeagnoidea* (A. Juss.) Benth.	Meliaceae	1							4	4	7							2		5	1
4	*Aidia pycnantha* (Drake) Tirveng.	Rubiaceae										2						1	1		1
5	*Albizia chinensis* (Osbeck) Merr.	Fabaceae									1	9						1			2
6	*Albizia lebbeck* (L.) Benth.	Fabaceae		1	5			1			6	37	5								
7	*Alphitonia philippinensis* Braid	Rhamnaceae		1	3			1				1									
8	*Alstonia scholaris* (L.) R. Br.	Apocynaceae			1		1				1	2									
9	*Antidesma bunius* (L.) Spreng.	Phyllanthaceae									2								1		
10	*Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery	Phyllanthaceae					21	1			38	1	2	3	3	10	7	1	3	1	
11	*Aralia vietnamensis* Ha	Araliaceae	1		1	1															
12	*Archidendron clypearia* (Jack) I.C.Nielsen	Fabaceae		1																	
13	*Archidendron lucidum* (Benth.) I.C.Nielsen	Fabaceae					6	1		10	16	3	9	4	13	3	3		2	2	1
14	*Artocarpus rigidus* Blume	Moraceae	1	1	1	4	1			2	1	3	1			1				1	1
15	*Azadirachta excelsa* (Jack) Jacobs	Meliaceae		2	10	1						4							3	1	
16	*Baccaurea ramiflora* Lour.	Phyllanthaceae	27	2	2	5		1	5	8	7	8	7	1	7	9	7	21	1		7
17	*Balakata baccata* (Roxb.) Esser	Euphorbiaceae	8	6	3	3		1	1			87						1			
18	*Barringtonia macrocarpa* Hassk.	Lecythidaceae		3																	
19	*Broussonetia papyrifera* (L.) L'HÃ©r. ex Vent.	Moraceae		1	1																
20	*Brucea javanica* (L.) Merr.	Simaroubaceae				16							1					1	1		
21	*Buchanania siamensis* Miq.	Anacardiaceae						1													
22	*Calophyllum calaba* L.	Calophyllaceae							1									2	2	2	
23	*Camellia forrestii* (Diels) Cohen-Stuart	Theaceae					1		1	1			2	2	3	11		2	1	1	
24	*Cananga latifolia* (Hook.f. & Thomson) Finet & Gagnep.	Annonaceae										1									
25	*Canarium album* (Lour.) DC.	Burseraceae									1					1					
26	*Canarium littorale* Blume	Burseraceae	4	1		2				3	1	3				1		1	1		
27	*Canarium pimela* K.D. Koenig	Burseraceae	1		2	4					1							3	3	3	
28	*Carallia brachiata* (Lour.) Merr.	Rhizophoraceae									9	2		1		1			3		

Table A2. *Cont.*

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
29	*Castanopsis piriformis* Hickel & A.Camus	Fagaceae			3	5	3				5	1		85		20	8	2			3
30	*Cinnamomum bejolghota* (Buch.-Ham.) Sweet	Lauraceae	1																		1
31	*Cinnamomum iners* Reinw. ex Blume	Lauraceae	29	3	12	5	1	1		21	9	3	5	2	2			12	19	4	11
32	*Cinnamomum porrectum* (Roxb.) Kosterm.	Lauraceae						1													
33	*Citrus hystrix* DC.	Rutaceae			1	1										1					
34	*Clausena excavata* Burm. f.	Rutaceae	4	4		6	1														
35	*Colona erecta* (Pierre) Burret	Malvaceae	1	1	1		1		1	7	1		1		2	1		6	3	3	6
36	*Cratoxylum formosum* (Jack) Benth. & Hook. f. ex Dyer	Hypericaceae					4	8			2		26	18	4	17	7				
37	*Croton tiglium* L.	Euphorbiaceae	6	1	1	1					1	1						16	16	6	21
38	*Crypteronia paniculata* Blume	Crypteroniaceae					12	21					1	6	2		3				
39	*Dillenia ovata* Wall. ex Hook.f. & Thomson	Dilleniaceae					1	2										2	10	5	10
40	*Dimocarpus longan* Lour.	Sapindaceae	1				3	6				9			22	1	3	6	3		
41	*Diospyros buxifolia* (Blume) Hiern	Ebenaceae								1											
42	*Diospyros hasseltii* Zoll.	Ebenaceae	1						5		1	1							3	3	
43	*Dysoxylum loureirii* (Pierre) Pierre ex Laness.	Meliaceae	2		1	1			3	2											
44	*Elaeocarpus bojeri* R.E. Vaughan	Elaeocarpaceae										1	2								
45	*Elaeocarpus chinensis* (Gardner & Champ.) Hook. f. ex Benth.	Elaeocarpaceae				1												1			
46	*Elaeocarpus gagnepainii* Merr.	Elaeocarpaceae									1				1						
47	*Elaeocarpus griffithii* (Wight) A.Gray	Elaeocarpaceae						3			2	4	16	9	6	5	1		1		2
48	*Elaeocarpus harmandii* Pierre	Elaeocarpaceae														1					
49	*Elaeocarpus lanceifolius* Roxb.	Elaeocarpaceae										1									
50	*Elaeocarpus obtusus* Blume	Elaeocarpaceae							1												1
51	*Elaeocarpus stipularis* Blume	Elaeocarpaceae							2		1	1	12	2		8	3			1	
52	*Elaeocarpus tectorius* Poir.	Elaeocarpaceae	2	1	3	2			1	29	8		3	2				3	7	2	8
53	*Endospermum chinense* Benth	Euphorbiaceae									1		1								
54	*Engelhardtia serrata* Blume	Juglandaceae											1		1						
55	*Eurya japonica* Thunb.	Pentaphylacaceae												1	1	3		3	5	2	

Table A2. *Cont.*

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
56	*Eurya trichocarpa* Korth.	Pentaphylacaceae												4	1	1	3				
57	*Eurycoma longifolia* Jack	Simaroubaceae										1									
58	*Fagraea fragrans* Roxb. ex Carey & Wall.	Gentianaceae					3							18	41		1				3
59	*Ficus drupacea* Thunb.	Moraceae							1									1			
60	*Ficus fulva* Reinw.	Moraceae								1	3	30							1		
61	*Ficus hispida* L. f.	Moraceae		2																	
62	*Garcinia cochinchinensis* (Lour.) Choisy	Clusiaceae				2				2	2								2		5
63	*Garcinia fusca* Pierre	Clusiaceae												6	4	8	12			3	7
64	*Garcinia oblongifolia* Champ. ex Benth.	Clusiaceae	1	2								1	2					1	2	8	9
65	*Gardenia obtusifolia* Roxb. ex Hook.f.	Rubiaceae	3	2		2				1	3							2			
66	*Gironniera subaequalis* Planch.	Cannabaceae	5		3					1	2	8							2	2	8
67	*Glochidion zeylanicum* (Gaertn.) A. Juss.	Phyllanthaceae	1	5	3	11		4		4	18	3						1			
68	*Gonocaryum lobbianum* (Miers) Kurz	Cardiopteridaceae							2	1											1
69	*Grewia asiatica* L.	Malvaceae	1	3																	
70	*Grewia tomentosa* Juss.	Malvaceae									1			1				1	2		1
71	*Helicia formosana* Hemsl.	Proteaceae						10							1	4					
72	*Hibiscus squamosus* Hochr.	Malvaceae	1		1								3	1							
73	*Homalium cochinchinensis* (Lour.) Druce	Salicaceae			1							2									
74	*Horsfieldia amygdalina* (Wall.) Warb.	Myristicaceae						1													
75	*Hymenodictyon orixense* (Roxb.) Mabb.	Rubiaceae												1							
76	*Ilex godajam* (Colebr. ex Wall.) Wall. ex Hook. f.	Aquifoliaceae					1	6						1		11	1			2	
77	*Kibatalia laurifolia* (Ridl.) Woodson	Apocynaceae	6						1											1	
78	*Knema furfuracea* (Hook. f. & Thomson) Warb.	Myristicaceae					3				2		1	2	1	6	2	1		1	1
79	*Knema globularia* (Lam.) Warb.	Myristicaceae					1														

Table A2. *Cont.*

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
80	*Lagerstroemia micrantha* Merr.	Lythraceae			4						21		1							2	1
81	*Lannea coromandelica* (Houtt.) Merr.	Anacardiaceae			4						3							1			
82	*Lithocarpus braianensis* A.Camus	Fagaceae							1		3		2								1
83	*Lithocarpus dealbatus* (Hook. f. & Thomson ex Miq.) Rehder	Fagaceae	1				4	7	1	8	2	4	21	3	29	12	1	1	6	1	6
84	*Lithocarpus echinotholus* (H.H. Hu) Chun & C.C. Huang	Fagaceae									1		1			1					
85	*Lithocarpus gigantophyllus* (Hickel & A. Camus) A. Camus	Fagaceae									6		1				2	1	2	2	3
86	*Lithocarpus truncatus* (King ex Hook. f.) Rehder & E.H. Wilson	Fagaceae	2	4	2		1		1		3			1			1	12	21	15	25
87	*Litsea auriculata* S.S. Chien & W.C. Cheng	Lauraceae									2										
88	*Litsea balansae* Lecomte	Lauraceae	1	6	2		1	12	4			5	1	4	1		2	1		8	
89	*Litsea cubeba* (Lour.) Pers.	Lauraceae				3															
90	*Litsea elongata* (Nees) Hook. f.	Lauraceae												3							
91	*Litsea glutinosa* (Lour.) C.B. Rob.	Lauraceae	1	2		6			9	1		2	1	2	1			5	3	4	8
92	*Litsea lancifolia* (Roxb. ex Nees) Benth. & Hook. f. ex Fern.-Vill.	Lauraceae									1										1
93	*Litsea martabanica* (Kurz) Hook. f.	Lauraceae							2				1								
94	*Litsea monopetala* (Roxb.) Pers.	Lauraceae										3	3			1					
95	*Litsea rotundifolia* Hemsl.	Lauraceae			1			6			1	1			6	5					
96	*Macaranga trichocarpa* (Zoll.) Müll.Arg.	Euphorbiaceae	1	121	17	80		1	124	1	1	2						2	1		5
97	*Magnolia braianensis* (Gagnep.) Figlar	Magnoliaceae										1						5	9	6	
98	*Magnolia mediocris* (Dandy) Figlar	Magnoliaceae	1						1		9				1					2	
99	*Mallotus barbatus* Müll.Arg.	Euphorbiaceae		15		15			2			8						2	1	5	1
100	*Mallotus philippensis* (Lam.) Müll. Arg.	Euphorbiaceae	23	9	11	6			8			2						4		1	3
101	*Mangifera odorata* Griff.	Anacardiaceae										3				2					
102	*Melicope pteleifolia* (Champ. ex Benth.) T.G. Hartley	Rutaceae	1		4						1		6	2		2	1				1

Table A2. *Cont.*

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
103	*Memecylon scutellatum* (Lour.) Hook. & Arn.	Melastomataceae	1					1		2	1	1		1				3	2		
104	*Millettia nigrescens* Gagnep.	Fabaceae									1										1
105	*Neolitsea ellipsoidea* C.K. Allen	Lauraceae	14	1	10	3				2		3		2			1		16	16	6	
106	*Ocotea lancifolia* (Schott) Mez	Lauraceae	23	3	10			3	1	4		16	8	8	2	3	1	16	11	5	4
107	*Ormosia sumatrana* (Miq.) Prain	Fabaceae						3					1		1				3		
108	*Parinari anamensis* Hance	Chrysobalanaceae									4										
109	*Peltophorum dasyrrhachis* (Miq.) Kurz	Fabaceae			1								1								
110	*Phoebe angustifolia* Meisn.	Lauraceae			12		2	9		20	27	101	9	14	12	10	2	13	2	7	12
111	*Phoebe macrocarpa* C.Y. Wu	Lauraceae			4					8	3							1	1		
112	*Phyllanthus reticulatus* Poir.	Phyllanthaceae									2										
113	*Polyalthia cerasoides* (Roxb.) Benth. & Hook. f. ex Bedd.	Annonaceae	3		1				3	3	1	1						9	1	11	5
114	*Premna mollissima* Roth	Lamiaceae			1											1					
115	*Prunus arborea* (Blume) Kalkman	Rosaceae	1		2					2	1							3	3		1
116	*Prunus phaeosticta* (Hance) Maxim.	Rosaceae						11							18	7	2				
117	*Psydrax dicoccos* Gaertn.	Rubiaceae	1																		
118	*Pterospermum heterophyllum* Hance	Malvaceae	2								3							1			
119	*Radermachera hainanensis* Merr.	Bignoniaceae	6		1					1	1	2						1	1		1
120	*Randia aculeata* L.	Rubiaceae	1		1	2															
121	*Rhodoleia championii* Hook. f.	Hamamelidaceae						5			4	1			44	5	75		2		2
122	*Schefflera heptaphylla* (L.) Frodin	Araliaceae	1		5		1						1	3	1	4	3	1	5	2	5
123	*Schima wallichii* (DC.) Korth.	Theaceae								20	4		14	3				1	11	16	13
124	*Stereospermum annamense* Dop	Bignoniaceae			1								1								
125	*Styrax tonkinensis* (Pierre) Craib ex Hartwich	Styracaceae			2		5	24		4	4	1	12	1	22	14	4				
126	*Syzygium chunianum* Merr. & L.M. Perry	Myrtaceae			10	2		16	3	45			3	3	4	3			15	8	18
127	*Syzygium cumini* (L.) Skeels	Myrtaceae						10								3					
128	*Syzygium lanceolatum* (Lam.) Wight & Arn.	Myrtaceae	3		2		13	5	1	31	9	3	3	14	3	5	6	7	23	44	31
129	*Syzygium levinei* (Merr.) Merr. & L.M. Perry	Myrtaceae									8					3			9	8	5

Table A2. *Cont.*

No	Species	Family	SF1 Plots						SF2 Plots									OGF Plots			
			1	2	3	4	5	6	1	2	3	4	5	6	7	8	9	1	2	3	4
130	*Terminalia bellirica* (Gaertn.) Roxb.	Combretaceae											1								
131	*Toona sureni* (Blume) Merr.	Meliaceae		1							1									2	
132	*Trema orientalis* (L.) Blume	Cannabaceae	1	8		64			20			1						6			
133	*Trevesia palmata* (Roxb. ex Lindl.) Vis.	Araliaceae	1						1												
134	*Triadica cochinchinensis* Lour.	Euphorbiaceae						10	3	1			2	2	4			2	6	5	6
135	*Vitex pinnata* L.	Lamiaceae							1					1		1	1				1
136	*Walsura pinnata* Hassk.	Meliaceae	2	3	3				5	2	3	1			1		10	20	7	12
137	*Wendlandia paniculata* (Roxb.) DC.	Rubiaceae						6	29		9		1	2	43	11	12			1	
138	*Xylopia vielana* Pierre	Annonaceae			1		2						11	8	14	5					1

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