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Phylogenetic diversity correlated with above-ground biomass production during forest succession: Evidence from tropical forests in Southeast Asia

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Abstract

1. Enhancing knowledge on the role of evolutionary history during forest succession and its relationship with ecosystem function is particularly relevant in the context of forest landscape restoration for climate change mitigation and adaptation.
2. We used fine resolution vegetation and environmental data (soil, elevation and slope) from two large-scale surveys (320 × 1000 m² plots in two 10 km × 10 km blocks) in the Upper Mekong to quantify (1) the role of abiotic and biotic (species interactions) factors in community assembly processes and (2) the effect of biodiversity, environmental factors and forest succession on above-ground biomass (AGB).
3. We found strong correlation between soil fertility and community structure in the early successional seres, while species interactions played an increasingly important role in older seres, presumably due to species complementary.
4. We detected a significant relationship between AGB and phylogenetic diversity, elevation and soil fertility across successional gradients. Within successional stages, soil fertility was not significantly associated with AGB, while elevation was significantly associated with AGB only in forest <100 years old. Phylogenetic diversity was positively correlated with AGB in the young secondary forest (< 15 years old) but not significantly associated with AGB in older seres.
5. *Synthesis.* Our results support the hypothesis that abiotic filtering influences species assembly in the initial stages of forest succession, while biotic interactions dominate community assembly processes in older seres. We found that phylogenetic diversity, soil fertility and elevation gradients were strongly predictive of AGB in a secondary tropical montane forest in Southeast Asia. However, elevation may reflect other underlying abiotic gradients, such as water availability. Phylogenetic diversity was significantly associated with AGB only in youngest

seres (<15 years old). Considering phylogenetic diversity in restoration plantings and the management of forests younger than 15 years old could enhance forest biomass and the climate mitigation function forest landscape restoration.

KEYWORDS

abiotic and biotic factors, above-ground biomass, biodiversity, community assembly, ecosystem function, phylogenetic diversity, succession, tropical forest

1 | INTRODUCTION

More than 150,000,000 ha of tropical forest were converted for farming between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013), with Southeast Asia (SE Asia) being at present the region with the highest deforestation rate globally (average 1% annually) (Miettinen, Shi, & Liew, 2011; Sodhi, Koh, Brook, & Ng, 2004). The conversion of tropical forest to monoculture plantations and farmlands has resulted in mosaic landscapes with various spatial arrangements of forests of widely varying age (Clough et al., 2016; Meyfroidt et al., 2014; Schmidt-Vogt et al., 2009). While it is generally acknowledged that secondary forests and farmlands do mitigate some of the biodiversity and ecosystem function losses (Chazdon, 2014), understanding how much and what type of biodiversity is needed to maintain ecosystem functioning remain key scientific questions (Brose & Hillebrand, 2016; Evans, 2016; Loreau, 2001; Midgley, 2012; Sutherland et al., 2013). Our study contributes directly to this body of knowledge by linking both evolutionary history (phylogenetic diversity and community structure) and ecosystem functioning to different successional forest phases in a mosaic landscape. This paper provides the first documentation of the relationship between phylogenetic diversity and tree above-ground biomass (AGB) during tropical forest succession in SE Asia.

Better understanding of the role of evolutionary history in the forest successional process and its relationship with ecosystem services, such as AGB accumulation as well as soil nutrient and physical quality, is particularly relevant in the context of forest landscape restoration initiatives aiming at mitigating climate change by sequestering carbon and restoring ecosystem functioning and productivity to degraded landscapes (Cadotte, Dinnage, & Tilman, 2012; Davies, Urban, Rayfield, Cadotte, & Peres-Neto, 2016; LaRue, Chambers, & Emery, 2017; Stockwell, Kinnison, Hendry, & Hamilton, 2016). As restoration requires decades, it is essential to predict restoration outcomes and tailor species selection as well as restoration activities accordingly (Khalil, Gibson, & Baer, 2016; Shooner, Chisholm, & Davies, 2015).

In the recent decades, ecologists have conducted over 500 experiments linking biodiversity with ecosystem functioning and it has recently been shown that biodiversity has a strong effect on ecosystem productivity, equivalent in size to the effects of climate and soil fertility (Duffy, Godwin, & Cardinale, 2017). Traditionally, ecologists have used species richness as the measure of biodiversity (Chiarucci, Bacaro, & Scheiner, 2011; Gotelli & Colwell, 2001;

Williams & Gaston, 1994). However, recent ecological studies have focused on partitioning different components of biodiversity, including evolutionary information and data on functional attributes, and using this information to infer ecosystem processes (Cavender-Bare, Kozak, Fine, & Kembel, 2009; Webb, Ackerly, McPeck, & Donoghue, 2002). This has enabled scientists to better understand how communities assemble by emphasising the long-term evolutionary history of coexisting species (Sardichanh, Millet, Heinemann, Nanthavong, & Harrison, 2015; Tucker et al., 2017).

Most research on forest successions focuses on the changes of phylogenetic structure and dispersion during succession (Chang, Zhou, & Peng, 2015; Letcher, 2010; Mo, Shi, Zhang, Zhu, & Slik, 2013; Whitfield, Kress, Erickson, & Weiblen, 2012). Few studies have quantified the relationship between biodiversity and ecosystem function (particularly phylogenetic diversity and AGB) during succession in tropical forests (e.g. Lasky et al., 2014; Ouyang et al., 2016).

Scientists have questioned whether or not phylogenetic diversity might be a better predictor of ecosystem functioning, stability and biomass productivity than species richness or functional diversity (FD) (Cadotte, 2015b; Cardinale et al., 2015; Venail et al., 2015). Flynn, Mirotchnick, Jain, Palmer, and Naeem (2011) reported that phylogenetic diversity was a better predictor than FD of community biomass productivity. Similarly, many studies have revealed that phylogenetic diversity can explain ecosystem function (biomass accumulation), stability and community biomass productivity better than measures of species richness, because phylogenetic diversity contains more information about species complementarity through space and time (Cadotte et al., 2012; Davies et al., 2016; Faith, 1992; Gravel et al., 2012; Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012). For example, Lasky et al. (2014) found that phylogenetic diversity during early succession was strongly correlated with tree AGB in a tropical forest. Nonetheless, plant biomass production varies among phylogenetic groups (Genung, Schweitzer, & Bailey, 2014). Potter and Woodall (2014) reported that phylogenetic diversity was significantly associated with forest AGB across geographic regions in the United States, but this relationship decreased significantly as site productivity and live tree stocking increased. Pu, Daya, Tan, and Jiang (2014) also demonstrated that the relationship between phylogenetic diversity and biomass accumulation was non-linear in communities containing a large population of the competitively superior species. Nevertheless, plant AGB tends to increase rapidly early in forest succession (Li et al., 2017) but the rate of AGB accumulation may decrease as stand age increases, and AGB may

even decline in the oldest stands (Chazdon, 2014), depending on the interaction between tree mortality and diameter recruitment (Rozendaal & Chazdon, 2015), and how these may be determined by species richness and environmental factors (Álvarez-Dávila et al., 2017; Dossa et al., 2013).

Plant community assembly processes along successional trajectories are influenced by many factors simultaneously, such as edaphic and topographic heterogeneity, disturbance, niche limitation, dispersal (regional and local species pools) and speciation (Chazdon, 2014; Kraft, & Ackerly, 2014; Mori, Isbell, & Seidl, 2018; Vellend, 2010). Moreover, variation in plant community assembly during forest succession may result from either deterministic or stochastic processes, or both acting simultaneously (Chai et al., 2016; Måren, Kapfer, Aarrestad, Grytnes, & Vandvik, 2018). The relationship between phylogenetic diversity and ecosystem function is based on the assumption that functional differences between species show an evolutionary signal and that close relatives are more similar to one another than more distantly related species (Cadotte, 2015a). Theoretically, environmental filtering (abiotic) and exclusive interactions (biotic) shape community assembly patterns (Yang et al., 2014). Phylogenetic clustering suggests abiotic factors drive community assembly processes leading more closely related species to coexist. The closely related species co-occurring in the local community tend to share similar niches and phenotypes in a particular environment (Burns & Strauss, 2011). On the other hand, phylogenetic overdispersion suggests that exclusive biotic interactions dominate community assembly, leading more distantly related species to co-occur (Webb, Ackerly, McPeck, & Donoghue, 2002; Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004). Nevertheless, Gerhold, Cahill, Winter, Bartish, and Prinzing (2015) pointed out that closely related species within a group of coexisting species may not share similar traits. In ecological succession theory, phylogenetic clustering is expected in early seres (Helmus et al., 2010) and habitat filtering (sunlight, temperature, soil types) plays an important role in selecting species during colonisation (Maire et al., 2012; Zobel, 1992). Whereas, phylogenetic overdispersion is expected to dominate later successional seres, stages at which competitive exclusion governs species establishment (Letcher, 2010; Maire et al., 2012; Purschke et al., 2013; Roeder et al., 2015; Zobel, 1992). For example, Letcher et al. (2012) found strong evidence of phylogenetic clustering during early forest succession, which significantly declined during the successional process. They found similar results when they examined the phylogenetic dispersion patterns with stem size and age classes. From these results they concluded that abiotic filtering strongly dominated the plant community assembly in the early stages of succession and the role of biotic interactions increased in the later successional stages. However, some studies argue that changes in plant phylogenetic community structure during succession may not be caused only by environmental filtering and biotic interactions (deterministic factors), but can also be caused by stochastic factors (Martins et al., 2015; Mi et al., 2016). For example, Norden, Letcher, Boukili, Swenson, and Chazdon, (2012) found that demographic processes (mortality and recruitment) drove variation

in phylogenetic community structure across successional gradients at different temporal scales. Mi et al., (2016) found weak evidence of deterministic processes (species, functional and phylogenetic turnover) in plant community assembly during forest succession in Southeastern China. They suggested that the weak evidence for deterministic processes detected might result from the prevalence of stochastic processes, particularly priority effects and random immigration.

The present paper uses fine-grained vegetation and soil data from mosaic secondary forests in the Upper Mekong to investigate the role of environmental filtering and species interactions during forest succession and the effect of biodiversity, environmental factors, successional stage and their interactions on ecosystem function, focusing on the accumulation of above-ground biomass. In this study, we addressed the following questions:

1. Do environmental filtering and species interactions dominate community assembly in different successional forest phases? We hypothesised that environmental filtering influences community assembly early in forest succession leading to phylogenetic clustering, and that species interactions dominate communities in the later successional stages leading to phylogenetic overdispersion due to species complementarity.
2. Does phylogenetic diversity predict ecosystem functioning (AGB) during tropical forest succession better than species diversity and environmental factors (soil fertility, slope and elevation)? We hypothesised that phylogenetic diversity predicts ecosystem function (AGB) better than species diversity and environmental gradients early in forest succession when most of the lineages within assemblage are closely related and share similar niches.

2 | MATERIALS AND METHODS

2.1 | Study site

The current study was conducted in two sites, located in Muang Beng, Oudomxay Province (20.474921°N, 101.811132°E), Northern Lao PDR (Mbeng site) and Manlaxiang, Xishuangbanna (22.149645°N, 101.481629°E), Southwestern China (Manla site). Elevation and slope of sampling plots for the Mbeng site ranged from 611 m to 1,463 m and from 0 degrees to 37 degrees, respectively. At the Manla site, elevation ranged from 811 m to 1,491 m and slope from 0 degrees to 43 degrees, respectively. Both Mbeng and Manla sites have a similar climate and forest types (tropical montane forest and secondary seasonal tropical forest), with mean annual rainfall of 1546 mm and 1,493 mm, respectively, of which 80% occurs during the wet season from May to October (Cao, Zou, Warren, & Zhu, 2006; Zhang & Cao, 1995). A variety of land-use types were present at both sites including arable land, long-term fallows, rubber plantations, secondary forests and old growth forests. A large proportion of the forested areas in both sites were dominated by *Fagaceae* species.

2.2 | Soil sampling and floristic data

Field surveys were carried out in 2014 and 2015, applying the Land Degradation Surveillance Framework (LDSF) methodology (Vågen, Winowiecki, & Jerome, 2013), implemented as part of the Sentinel Landscape Project under the Forests, Trees and Agroforestry research programme of the Consultative Group on International Agricultural Research (CGIAR).

The sampling design for vegetation surveys and soil sampling followed the standard LDSF protocol (Vågen, Winowiecki, & Jerome, 2013), which has been implemented in a number of projects and studies in the global tropics (Abegaz, Winowiecki, Vågen, Langan, & Smith, 2016; Vågen, Winowiecki, Abegaz, & Hadgu, 2013; Winowiecki, Vågen, & Huising, 2016). Each LDSF site is a 10 km × 10 km block, which is divided into 16 panels with a cluster of 10 randomly assigned plots within a 1 km radius of the centre of the panel. Each plot represents a 1,000 m² sampling area and consists of four subplots (giving a total of 160 plots and 640 subplots per site). Subplot 1 is placed at the centre of the plot, with the remaining subplots positioned in a Y-shape with the horizontal distance from the centre of subplot 1 to the centre of each of the other subplots being 12.2 m. Each subplot is a circular plot with a radial distance of 5.64 m, thus covering a 100 m² area. Subplot 2 is always positioned downslope, while subplots 3–4 are positioned 120 degrees and 240 degrees upslope, respectively. A circle describing the perimeter of all four subplots covers an area of 1,000 m². For each subplot, coordinates, elevation, slope, topographic position, land-use history, woody and herbaceous vegetation structure, visible erosion (rill, gully and sheet) and rock/stone cover rate are recorded. Human impacts from agriculture, tree cutting, fire, flooding, erosion, firewood collection, etc. are also noted. Soil samples are collected from the centre of each subplot. For our sites, all trees with diameter at breast height (dbh) ≥ 5 cm were identified and measured for dbh and height. Herbarium specimens were collected for species unidentified in the field.

Topsoil samples were collected at 0–20 cm and subsoil samples at 20–50 cm depth. Soil field texture was determined for each subplot for both topsoil and subsoil, and soil collected from all four subplots were composited into one topsoil sample and one subsoil sample for each LDSF plot.

We classified forest successional stage according to plot land use and disturbance history. The successional stages used in this study were (a) secondary forest <15 years old (SFI); (b) secondary forest 15–30 years old (SFII); (c) secondary forest 30–100 years old (SFIII) and (d) old growth forest >100 years old (OGF). Successional stage was assigned at the subplot level, although usually all four subplots within a plot were the same. Cropland, fallow-land and plantation plots were excluded from this study.

2.3 | Mid Infrared (MIR) diffuse spectroscopy of soil samples

All soil samples were air-dried for a minimum of 7 days in 20°C and air-dried subsamples (15 g) were ground for 2 min in a mortar grinder

RM200 (Milling Machine, Retsch®) followed by gently crushing to pass through a 0.15 mm sieve. We analysed 10% of the collected soil samples using traditional methods (wet chemistry) at the Biogeochemical Laboratory (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences) in order to have a reference dataset for model calibration of the spectroscopy for each chemical element (see Appendix S1). These 10% samples represented 32 samples from each site and were selected from the first plot of each cluster that had both top and sub-soil samples. Air-dried and ground samples were scanned in the MIR from 4,000 to 400 per cm or 2,500 to 25,000 nm; each scanned soil sample was read into R via a script developed by the World Agroforestry Centre (ICRAF) and these spectra were digitally converted to a.csv file through the package hexView in R (Murrell, 2015). All spectra were used for calibration models using the *train* function from caret package (Kuhn, 2008) based on the method using the random forest (RF) algorithm. The calibration consists in creating two sets (a) training set and (b) testing set (Tables S1 and S2). Then, we used the best-calibrated models to predict (*predict* function) the soil minerals contents and soils properties of all soil samples (see Appendix S1 for the detail of soil MIR spectroscopy). Seven soil fertility indicators: total Nitrogen (TN), total Phosphorus (TP), total Sulfur (TS), Organic Carbon (OC), total Potassium (TK), total Iron (TFe) and pH were selected for further analysis in this study (see Figure S1 for summary of the soil properties).

2.4 | Phylogeny reconstruction

All tree species names were standardised following The Plant List (<http://www.theplantlist.org/>) and Taxonomic Name Resolution Service v4.0 (Boyle et al., 2013, <http://tnrs.iplantcollaborative.org>) to check whether the species names match with Angiosperm Phylogeny Group III (APG III, 2009). Next, a phylogeny of each site (Figures S2 and S3) was built using Phylocom software v4.2 (Webb, Ackerly, & Kembel, 2008). Each phylogeny was constructed based on Megatree R20120829 for plants in Phylomatic v3 as a backbone. The phylogeny in Newick format was generated using Phylomatic's online tools (<http://phylodiversity.net/phyloomatic>). We then used the *bladj* algorithm in Phylocom to assign branch lengths and add node ages following Wikstrom, Savolainen, and Chase (2001).

2.5 | Data analysis

2.5.1 | Phylogenetic community structure and diversity analysis

To examine phylogenetic community structure, we first calculate mean pairwise distance (MPD) weighted by species relative abundance. Abundance-weighted is the most informative way to access ecosystem functioning of co-occurring species and test whether species abundance influences community phylogenetic structure (Khalil et al., 2016; McCoy & Matsen, 2013; Tucker et al., 2017). After that, we calculate the net relatedness index (NRI) of each community following the Equation 1:

$$\text{NRI} = -((\text{MPD}_{\text{obs}} - \text{MPD}_{\text{rd}}) / \text{MPD}_{\text{sd}}) \quad (1)$$

where obs is the observed MPD, rd is the mean random MPD and sd is the standard deviation of MPD among the null communities. MPDs were calculated from 999 randomly assembled communities (holding the species-abundance distribution constant and randomly assigning occurrence in plots) using the *ses.mpd* function of picante package (Kembel et al., 2014) in R. Negative NRI values indicate overdispersion while positive values indicate clustered phylogenetic community structure, respectively (Webb, Ackerly, McPeck, & Donoghue, 2002). We examined the relationship between NRI and soil principle component analysis (PCA) axes of each successional stage to derive information concerning the community assembly processes.

We examine phylogenetic diversity using phylogenetic species richness (PSR) metric proposed by Helmus, Bland, Williams, and Ives (2007) not Faith's PD (Faith, 1992), because PSR measures the evolutionary dissimilarity of the species within an assemblage based on pair-wise distance and phylogenetic variability, and can be weighted by species richness which was more interesting to us than the amount of the evolutionary history along a phylogeny measured by Faith's PD (Faith, 1992; Helmus et al., 2007; Tucker et al., 2017). PSR is calculated from the phylogenetic species variability and species richness in an assemblage. We calculated PSR using *psd* function. We then generated PSR rarefaction curves using the *specaccum.psr* function. Phylogenetic analyses were performed using picante (Kembel et al., 2010) and ape packages in R (Paradis, Claude, & Strimmer, 2004). We calculated species diversity across plots using Fisher's alpha index (Fisher, Corbet, & Williams, 1943). Fisher's alpha was calculated using *fisher.alpha* function in the vegan package (Oksanen et al., 2018).

2.5.2 | Species co-occurrence pattern and community structure

To examine whether species interactions dominate co-occurrence patterns during succession, we first calculated the Checkerboard score (C-score) proposed by Stone and Roberts (1990) based on the binary presence and absence community matrix. We used SIM9 randomisation algorithm (Connor & Simberloff, 1979) for C-score calculation as recommended by Gotelli (2000). We then examined the species co-occurrence pattern of each successional stage from 1,000 randomly assembled communities, using the *cooc_null_model* function from EcoSimR package (Gotelli, Hart, & Ellison, 2015) to generate the null communities. Next, the standardised effect size of C-score (SES_C) for each successional stage was calculated to test for significance ($p < 0.05$) (Gotelli & McCabe, 2002; Gurevitch, Morrow, Wallace, & Walsh, 1992); the non-significant SES_C values (95% of the observation) will fall between -2 and 2 ($\text{SES}_C > 2$ significantly greater than expected, $\text{SES}_C < -2$ significantly less than expected). SES_C was calculated according to Equation 2:

$$\text{SES}_C = (I_{\text{obs}} - I_{\text{sim}}) / \text{SD}_{\text{sim}} \quad (2)$$

where I_{obs} is the observed index, I_{sim} is the simulated index of null assemblages and SD_{sim} is the standard deviation of simulated null assemblages. To indicate competitively structured community, we expected SES_C values > 2 (Gotelli, 2000; Gotelli & McCabe, 2002).

2.5.3 | Tree above-ground biomass

To access ecosystem function in a given community, we estimated the AGB of each plot. We first obtained wood density data for all tree species using *getWoodDensity* function in BIOMASS package (Réjou-Méchain, Tanguy, Pioniot, Chave, & Hérault, 2017), based on the global wood density database (Chave et al., 2009; Zanne et al., 2009). We then calculated AGB using the Equation 3 from Chave et al. (2014):

$$\text{AGB} = 0.0673 \times (\text{WD} \times H \times \text{dbh}^2)^{0.976} \quad (3)$$

where WD is wood density (g/cm³), H is tree height (m) and dbh is diameter at breast height (cm). Leaning and broken top trees were excluded from analysis. The total AGB value of each plot was used for further analysis.

2.5.4 | Soil principle component analysis

Principle component analysis was applied on the seven selected soil fertility parameters from each site to reduce the number of parameters. We first standardised and scaled (mean = 0 and standard deviation = 1) data as suggested by Venables and Ripley (2003).

2.5.5 | Null model

To investigate whether phylogenetic diversity increased or decreased during forest succession, and whether phylogenetic community structure patterns were phylogenetically clustered (more similar than expected by chance) or overdispersed (less similar than expected by chance) at each successional stage, we used null model 1a from Hardy (2008) that maintains the abundance and frequencies of species co-occurrence at each site and among sites along the phylogeny (Hardy, 2008; Shooner et al., 2015). For phylogenetic community structure (NRI), we used the *richness* null model in the function *ses.mpd* of picante package (Kembel et al., 2010). This null model randomises the community data matrix based on the species abundance and maintains species richness across the phylogeny.

2.5.6 | Statistical analyses

Pearson's correlation coefficient was used to test the correlation between NRI values and soil PCA axes. To examine whether PSR, species diversity (Fisher's alpha), environmental factors (soil fertility, slope and elevation gradients), successional stage

and their interactions predicted community biomass, and to account for the spatial autocorrelation among successional stages, we used generalised least squares (GLS) to fit linear models using *gls* function in nlme package (Pinheiro et al., 2017). We tested spatial autocorrelation using the variogram function. We then fitted our models with different correlation structures and compared models using Akaike's Information Criterion (AIC) and the model with the lowest AIC value was selected. We found that the model with a spherical correlation structure has a lowest AIC score. We checked the normality of the model residuals using *qqPlot* function in ggplot2 package (Wickham, 2009). We then observed relationships of the AGB and phylogenetic diversity, species diversity and environmental gradients within each successional stage using simple linear regression. We used structural equation modeling (SEM) to examine direct and indirect effects of PSR, species diversity and environmental factors on AGB using the *sem* function in the lavaan package (Rosseel, 2012). Maximum likelihood was used to estimate the model parameters and standard errors were bootstrapped 1,000 times. SEM models were compared using AIC and goodness-of-fit index (GFI) (Hoyle, 2012), the model with lowest AIC and GFI > 0.95 was selected. All of the data analyses were performed in R version 3.4.0 (R Core Team, 2017).

3 | RESULTS

3.1 | Plant community

In the Mbeng site, a total of 3,667 individual trees were measured, belonging to 164 species, 104 genera and 42 families. In the Manla site, a total of 4,825 individual trees of 220 species, 113 genera and 50 families were measured. Cropland and rubber plantation plots were excluded from further analyses, resulting in a reduction of seven species at Mbeng and 13 species at Manla.

3.2 | Soil principle component analysis (PCA)

The first three PCA axes of Mbeng and Manla sites accounted for 95.3% and 89.3% of the variance in soil parameters, respectively; and were used to indicate soil fertility for further analysis (Figure 1). At Mbeng, PCA axis 1 (PCA1) accounted for 50% of the total variance in measured soil gradients at this site, and was positively associated with TN, TP, TS and OC; PCA axis 2 (PCA2, accounting for 29.3%) was positively associated with TK and TFe; and PCA axis 3 (PCA3, accounting 16%) was negatively associated with pH. At Manla, PCA1 explained 40% of total variance in the selected soil fertility parameters and was positively correlated with TK, pH, and negatively associated with OC and TN; PCA2 (accounting for 30%) was positively

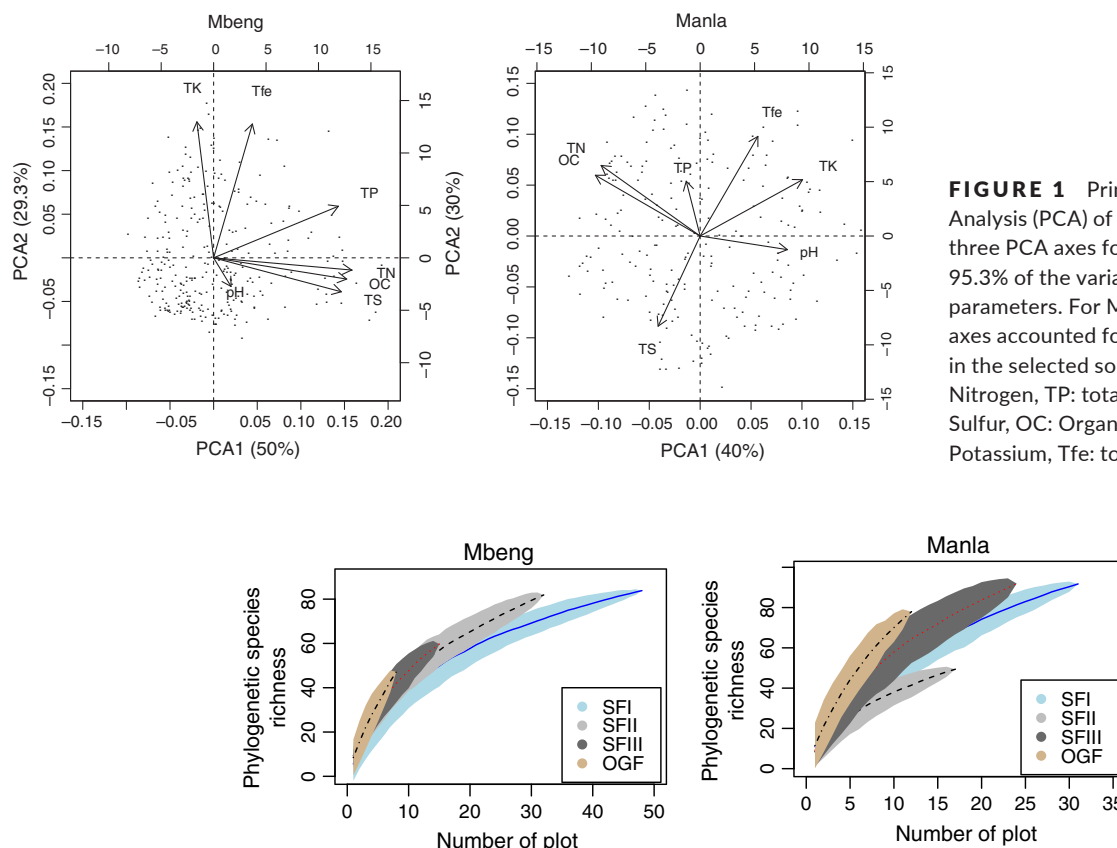


FIGURE 1 Principle Component Analysis (PCA) of soil variables. The first three PCA axes for Mbeng accounted for 95.3% of the variance in the selected soil parameters. For Manla, the first three axes accounted for 89.3% of the variance in the selected soil parameters. TN: total Nitrogen, TP: total Phosphorus, TS: total Sulfur, OC: Organic Carbon, TK: total Potassium, TFe: total Iron

FIGURE 2 Phylogenetic Species Richness (PSR) curves of each successional stage: secondary forest < 15 years old (SFI), secondary forest 15–30 years old (SFII), secondary forest 30–100 years old (SFIII) and old growth forest >100 years old (OGF). These PSR curves showed that phylogenetic diversity increases with successional stage (although the least diverse community in Manla was SFII rather than SFI) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Standardised effect size values of C-score (SES_C) generated from 1,000 simulated communities of each successional stage: secondary forest <15 years old (SFI); secondary forest 15–30 years old (SFII); secondary forest 30–100 years old (SFIII) and old growth forest > 100 years old (OGF)

Successional stage	Mbeng			Manla		
	Observed index	SES_C	<i>p</i> value	Observed index	SES_C	<i>p</i> value
SFI	10.72	0.51	0.26	9.36	0.47	0.37
SFII	4.35	4.51	<0.001	4.42	7.16	<0.001
SFIII	2.44	0.006	0.4	1.7	2.84	<0.001
OGF	4.76	2.17	0.007	1.59	2.5	<0.001

Note. Bold values are statistically significant ($p < 0.05$).

associated with TFe, TN, OC, TP and TK, but negatively associated with TS; and PCA3 (accounting for 19.3%) was negatively associated with TP and pH.

3.3 | Phylogenetic diversity and community structure

Net relatedness index values of the early forest successional stage (SFI) were positive, indicating phylogenetic clustering but these decreased to negative in OGF. As expected, we detected only negative NRI values for OGF, indicating phylogenetic overdispersion of late successional communities. PSR curves indicated that phylogenetic diversity increased with forest age (successional stage) (Figure 2).

3.4 | Species co-occurrence pattern and community structure

The standardised effect size of C-score values for the SFI successional stage were not significant at both of our study sites and the SES_C value for SFIII was not significant for the Mbeng site. However, the remainder of the SES_C values were significantly greater than expected (observed metric > simulated metric; $SES_C > 2$; $p < 0.05$), suggesting competitively structured communities (more detail see Table 1).

3.5 | Correlation between soil fertility and community structure

Pearson's correlation tests revealed a strong correlation between NRI values of Mbeng SFI successional stage with PCA1 ($R^2 = 0.37$, $p = 0.01$) and PCA3 ($R^2 = 0.29$, $p = 0.04$), and between Manla SFI and SFII successional stages with PCA1 (SFI $R^2 = -0.38$, $p = 0.03$; SFII $R^2 = -0.45$, $p = 0.04$). There were no other significant correlations between NRI and soil parameters for the remaining successional stages (Table 2). These results were based on the predicted soil parameters derived from modelling the soil spectra; however, similar results were obtained when we used only the 10% wet chemistry calibration samples.

TABLE 2 Pearson's correlation between Net Relatedness Index (NRI) values of each successional stage (secondary forest <15 years old (SFI); secondary forest 15–30 years old (SFII); secondary forest 30–100 years old (SFIII) and old growth forest >100 years old (OGF)) and soil principle component analysis (PCA) axes. NRI values of Mbeng SFI successional stage were correlated with PCA1 and PCA3. Manla NRI values of SFI and SFII successional stages were negatively correlated with PCA1

NRI	Mbeng			Manla		
	PCA1	PCA2	PCA3	PCA1	PCA2	PCA3
SFI	0.37**	-0.27	0.29*	-0.38**	0.06	-0.15
SFII	0.22	-0.33	-0.16	-0.45*	-0.27	0.05
SFIII	0.006	-0.01	0.48	-0.18	0.22	0.04
OGF	-0.58	-0.005	-0.17	0.15	0.43	0.19

Note. Bold values are statistically significant at $p < 0.05$ with * for $p = 0.04$ and ** for $p < 0.04$.

3.6 | Phylogenetic diversity, environmental gradients and above-ground biomass

Phylogenetic species richness, soil fertility (PCA2) and elevation were significantly associated with community AGB across successional stages (PSR: estimate (Est) = 0.07, standard error (SE) = 0.01, $T = 3.94$, $p = 0.0001$; PCA2: Est = -0.17, SE = 0.05, $T = -3.05$, $p = 0.002$; elevation: Est = 0.002, SE = 0.0004, $T = 5.93$, $p < 0.0001$), but we did not detect any significant relationship between species diversity (Fisher's alpha) and slope with AGB.

Within a successional stage, PSR and total AGB were strongly correlated with early successional communities (SFI $R^2 = 0.30$, $T = 5.82$, $p < 0.0001$), but not in older communities (SFII $R^2 = 0.002$, $T = 0.33$, $p = 0.73$, SFIII $R^2 = 0.8$, $T = 1.86$, $p = 0.07$ and OGF $R^2 = 0.004$, $T = 0.26$, $p = 0.79$) (Figure 3). Similarly, elevation was strongly correlated with total AGB (Figure 4) early in succession (SFI $R^2 = 0.30$, $T = 5.75$, $p < 0.0001$), while this relationship was weaker (but still significant) in the SFII and SFIII successional stages and non-significant in the old growth communities (SFII $R^2 = 0.09$, $T = 2.28$, $p = 0.026$; SFIII $R^2 = 0.12$, $T = 2.26$, $p = 0.02$; OGF $R^2 = 0.005$, $T = 0.3$, $p = 0.76$). We did not detect any

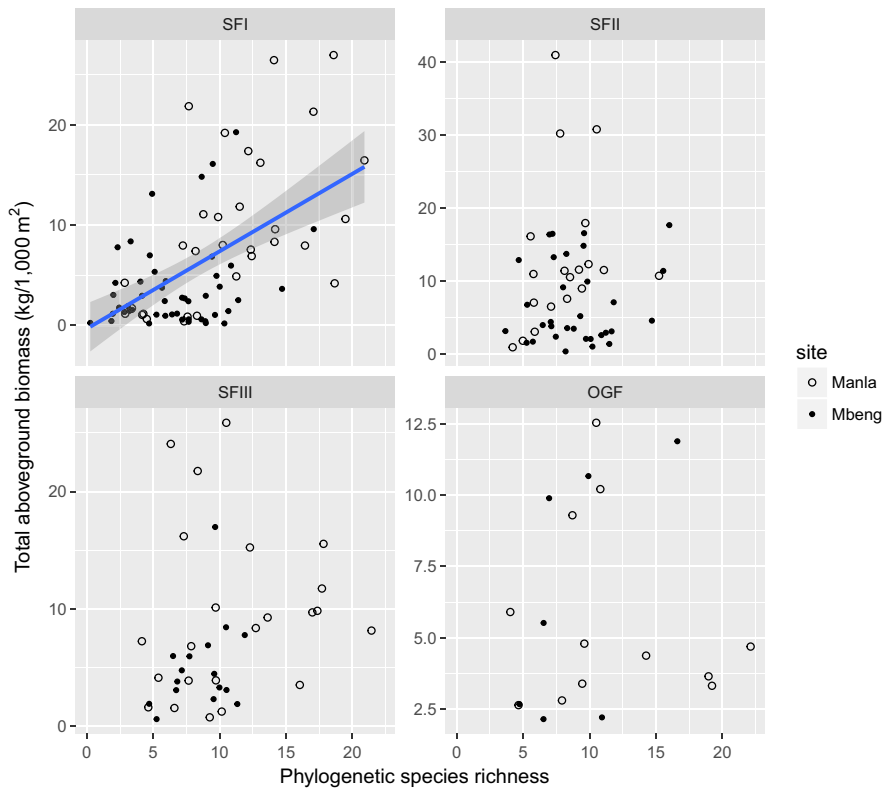


FIGURE 3 Relationship between Phylogenetic species richness (phylogenetic diversity) and total above-ground biomass (AGB) within each successional stage. Phylogenetic diversity and total AGB of the secondary forest <15 years old (SFI) were significantly positive correlated ($R^2 = 0.30$, $T = 5.82$, $p < 0.0001$), but older communities were not: secondary forest 15–30 years old (SFII: $R^2 = 0.002$, $T = 0.33$, $p = 0.73$), secondary forest 30–100 years old (SFIII: $R^2 = 0.8$, $T = 1.86$, $p = 0.07$) and old growth forest >100 years old (OGF: $R^2 = 0.004$, $T = 0.26$, $p = 0.79$) [Colour figure can be viewed at wileyonlinelibrary.com]

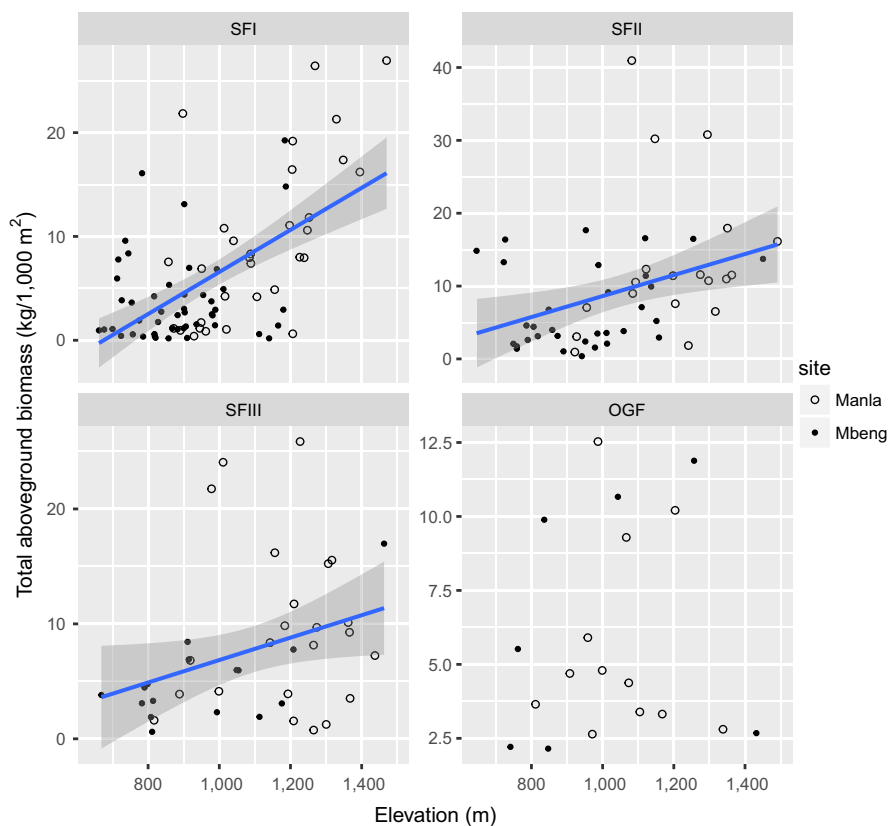


FIGURE 4 Relationship between elevation and total above-ground biomass (AGB) within each successional stage. Elevation and total AGB were strongly positive correlated in the secondary forest <15 years old (SFI: $R^2 = 0.30$, $T = 5.75$, $p < 0.0001$), but weaker in the secondary forest 15–30 years old (SFII: $R^2 = 0.09$, $T = 2.28$, $p = 0.026$) and secondary forest 30–100 years old (SFIII: $R^2 = 0.12$, $T = 2.26$, $p = 0.02$); and non-significant in the old growth forest >100 (OGF: $R^2 = 0.005$, $T = 0.3$, $p = 0.76$). [Colour figure can be viewed at wileyonlinelibrary.com]

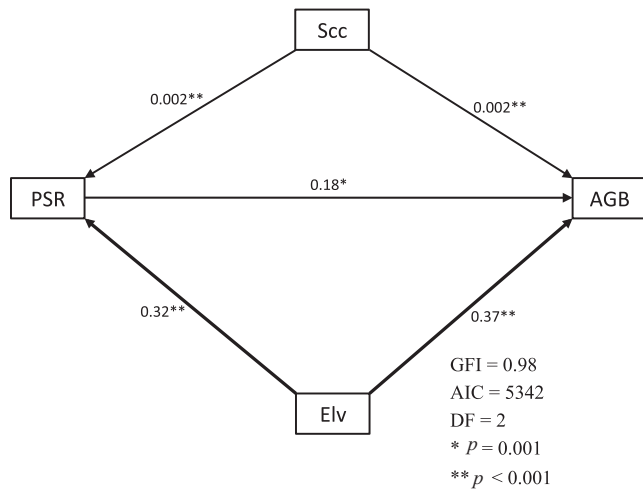


FIGURE 5 Structural Equation Model (SEM) paths showed direct and indirect effects of elevation (Elv), phylogenetic diversity (PSR) and successional stage (Scc) on above-ground biomass (AGB). The figure on each path is the standardised regression coefficient. The maximal model included PSR, successional stage, species diversity (Fisher's Alpha), soil fertility, elevation and slope. Non-significant coefficients paths ($p > 0.05$) were excluded from SEM diagram. The thickness of the arrow denotes the power of the correlation. DF: degree of freedom, GFI: goodness-of-fit index, AIC: Akaike's Information Criterion

significant relationship between soil fertility and total AGB within each successional stage.

The SEM detected significant direct and indirect (through PSR) effects of elevation and successional stage on AGB (Elevation: direct effect $p < 0.001$, effect = 0.37; indirect effect $p < 0.001$, effect = 0.32; Succession: direct effect $p < 0.001$, effect = 0.002; indirect effect: $p < 0.001$, effect = 0.002). We also detected a significant direct effect of PSR on AGB: $p = 0.001$, effect = 0.185 (Figure 5).

4 | DISCUSSION

Our results show clear patterns of change in the phylogenetic community structure during forest succession, and support the hypothesis that environmental filtering influences species assembly during early succession, as evidenced by lower phylogenetic diversity, phylogenetic clustering and strong correlation between phylogenetic community structure and soil fertility. Competitive exclusion became more important later in succession, as evidenced by higher phylogenetic diversity, phylogenetic overdispersion and competitively structured communities (C-score's SES values > 2) (Helmus et al., 2010; Letcher, 2010; Maire et al., 2012; Purschke et al., 2013; Roeder et al., 2015; Zobel, 1992).

Environmental filtering is expected to dominate species selection and colonisation early in the succession, resulting in a local community of closely related species (phylogenetic clustering) (Maire et al., 2012; Zobel, 1992). However, the importance of competition is

expected to increase with successional age, and indeed this is what occurred at both of our study sites (Mbeng and Manla). Our results showed that early successional seres contain more closely related species than expected by chance (phylogenetic clustering), and we detected a strong correlation between Net Related Index (NRI) values of the young secondary forest < 15 years old (SFI) successional stage and soil fertility. However, the phylogenetic community structure shifted from clustering to overdispersion in the secondary forest 15–30 years old (SFII) and secondary forest 30–100 years old (SFIII) successional stages, while OGF showed only phylogenetic overdispersion. C-score's SES values also confirmed competitively structured communities in the SFII, SFIII and OGF successional stages. At the same time, we did not detect correlation between the NRI of SFII (Mbeng), SFIII, OGF and soil fertility (PCA axes). Hence, we conclude that competitive exclusion dominated community assembly in the older forest seres.

We detected a significant relationship between total AGB and phylogenetic diversity, elevation and soil fertility across successional gradients. Within each successional stage, however, we failed to detect significant relationships between soil fertility and total AGB. Nonetheless, we detected a significant relationship between total AGB and elevation gradients in the SFI, SFII and SFIII successional stages, but this was non-significant in OGF communities. This result is consistent with previous studies, which show that elevation is one of the main environmental factors predicting above-ground carbon stock in tropical forests and significantly shapes patterns of species diversity and distribution (Dossa et al., 2013; Marshall et al., 2012; Molina-Venegas, Aparicio, Lavergne, & Arroyo, 2016; Pottier et al., 2013). Many studies have reported that forest biomass decreases as elevation increases (Dossa et al., 2013; Fadrique & Homeier, 2016; Girardin et al., 2014). Our results suggested that elevation gradients significantly affect tree biomass only for communities less than 100 years old, but that AGB in OGF was unrelated to elevation. However, it must be cautioned that the form of measured ecological responses to abiotic gradients will depend on the range included in a study, which for elevation in this study was less than 1,500 m. Hence, what is interesting to report here is the declining importance of elevation as a predictor of AGB with forest age, rather than the significance or not thereof. It should also be understood that, as an observational result, elevation may be a proxy for underlying environmental drivers, such as water availability. For example, Álvarez-Dávila et al. (2017) reported that climatic factors (particularly water availability) strongly shaped AGB production in the OGF across South America, while water availability significantly affected the AGB recovery of the secondary growth forest (Poorter et al., 2016). Within each successional stage, phylogenetic diversity (using here PSR) was positively correlated with community total AGB only in the first 15 years of forest succession but was non-significant in the older successional communities. PSR has two components, phylogenetic variability and species richness. This result is concordant with Steudel et al. (2016) and Lasky et al. (2014), who found that the relationship between biomass productivity and phylogenetic diversity was strongly driven by species richness and shifted from positive to

negative or non-significant during forest succession. Mori, Osono, Cornelissen, Craine, and Uchida (2017) confirmed that the relationship between biodiversity and ecosystem function started from early on in primary succession.

Meanwhile, Cadotte (2013) reported that communities that contained more distantly related species or were phylogenetic overdispersed (later in the forest succession) tended to have higher biomass production, and suggested that this was a consequence of species complementary. The positive relationship between phylogenetic diversity and biomass (ecosystem function) can be found via sampling effects when the most productive species are included in the community (Davies et al., 2016; Naeem et al., 1999) across trophic levels and vary for different land use types or in fragmented landscapes (Peralta, Frost, Didham, Varsani, & Tylianakis, 2015; Thompson, Davies, & Gonzalez, 2015). Our results are in line with Lasky et al. (2014) who found a positive correlation between phylogenetic diversity/functional diversity and AGB in the early stages of forest succession, but contrast with those of Ouyang et al. (2016) who did not detect a relationship between phylogenetic diversity and AGB during succession in a subtropical forest in China. However, Ouyang et al. (2016) classified forest successional stages based on species composition while both our study and Lasky et al. (2014) classified successional stages based on forest age and land-use history. Recent studies have argued whether or not phylogenetic diversity is a better predictor for ecosystem functioning than species richness or FD alone (e.g. Venail et al., 2015; Cadotte, 2015b; Steudel et al., 2016). For example, Yuan et al. (2016) and Venail et al. (2015) reported that phylogenetic diversity does not predict ecosystem functioning but taxonomic diversity and species richness do. However, a long-term experimental study published by Cadotte et al. (2012) revealed robust results that show and emphasise that phylogenetic diversity promotes ecosystem stability and community biomass productivity, although this could be explained by sampling effects. However, they also showed biomass variance declined with increasing phylogenetic diversity, which is best explained by complementarity effects. Larkin et al. (2015) reported results from a 25 year long dataset showing that phylogenetic diversity provided better information for management and restoration interventions than FD in a fire prone ecosystem, because phylogenetic diversity reflects species' response to environmental gradients through time (see also Barak et al., 2017; Barber et al., 2017; Shooner et al., 2015 for how phylogenetic diversity could play an important role in restoration and management). Although Cadotte, Davies, and Peres-Neto (2017) argue that a failure to detect a significant relationship between phylogenetic diversity and ecosystem function might be caused by inappropriate study design when considering the species pool, experimental design and analyses. Also, some studies that have concluded that competition was the major mechanism constructing communities did not consider the potential roles of "sampling effects" and "complementarity effects" (Loreau & Hector, 2001).

Our finding suggests that including a phylogenetic approach (phylogenetic diversity and community structure) in restoration plantings and management practices of the forest younger than 15 years old could enhance the climate mitigation function of these

forests across SE Asia. In conclusion, our study revealed a strong abiotic filtering influence on species assembly and colonisation early during forest succession, while competitive exclusion played an increasingly important role in the community assembly processes among older communities. Our results demonstrate that phylogenetic diversity, soil fertility and elevation gradients were strongly predictive of AGB during forest succession in a tropical montane forest in SE Asia.

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AUTHORS' CONTRIBUTIONS

M.S. conducted fieldwork, collected plant and soil samples; performed plant identification for Mbeng site; conceived the ideas, analysis and led the writing of the manuscript. M.S. and G.G.O.D. processed soil samples. G.G.O.D., M.H., Y.K. prepared soil samples and carried out the soil MIR spectroscopy analysis. L.W. and T-G.V. developed methods, training and collaborated on fieldwork implementation. R.D.H. and M.S. conceived the study and collaborated on the analysis, and development of the manuscript. All the authors contributed critically to the revision and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this study are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6ns42cq> (Satdichanh et al., 2018).

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