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Untangling the impact of plantation type and functional traits on ecosystem nutrient stocks in an experimentally restored forest ecosystem

Liping Wei[a,*], Frédéric Gosselin[b]

[a] *CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*

[b] *INRAE, UR EFNO, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France*

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*Corresponding author

E-mail: liping.wei228@hotmail.com

Address: No.723, Xingke Road, Tianhe District, Guangzhou, 510650, China

Abstract

The primary objective of ecological restoration is recovering biodiversity and ecosystem functioning. While a functional trait-based approach can help understand community assembly and ecosystem function recovery during ecological restoration, there still exists a knowledge gap in assessing how functional traits indicate the mediating roles of the plant community in response to forest restoration effects on ecosystem functions. This study applied the "response-effect trait" framework to investigate experimentally whether the treatment of plantation type has an impact on community trait compositions, which in turn could affect forest ecosystem nutrient stocks – here, carbon (C) and nitrogen (N) and phosphorus (P) stocks in tree, understory, litter and soil pools at an experimental station in subtropical China. We used structural equation models (SEMs) to examine the relationships among plantation type, community weighted mean of traits, and nutrient stocks in each pool. Our results show that most of the tree and understory traits studied were response traits to plantation type. Moreover, certain traits played a significant role in mediating plantation-type effects on C, N and P stocks for understory pool (e.g., understory stem specific density and specific leaf area, tree leaf phosphorus content), and for litter and soil pools (e.g., tree leaf carbon or phosphorus content, understory specific leaf area, leaf nitrogen or phosphorus content), known as "response-effect traits". For the tree pool, only effect traits, and no "response-effect" tree traits, were found for the N stock. Total effects of SEMs indicated that, understory or tree traits can have a greater impact than plantation type on understory or litter C, N or P stocks. After approximately 35 years of natural restoration, exotic plantations exhibited a different community trait characteristic from native plantations. The important roles of traits in mediating the effects of plantation type on non-tree pool C, N and P stocks were highlighted.

Key words: carbon and nitrogen stocks; functional traits; native and exotic plantations; tree and understory layers; ecological restoration

1. Introduction

The exploitation and alteration of natural environments by humans is causing a significant loss of biodiversity and a decline in ecosystem health, resulting in a reduction in the provision of ecosystem services (IPBES, 2019). Ecological restoration is a promising approach to restoring the functionality and integrity of degraded ecosystems (Romanelli, 2018). To date, the primary objective of ecological restoration has been to restore biodiversity and ecosystem functions, which is challenging due to the unpredictability of restoration outcomes (Choi, 2007; Rey Benayas, et al., 2009; Suding, 2011). To increase the predictability of restoration effects, it is essential to explore and better understand the community composition and ecosystem functioning in the restoration process, since this will help identify common patterns and mechanisms across different restoration studies.

The functional trait-based approaches is valuable for comprehending the processes of community assembly and ecosystem functions in restoration contexts. Functional traits represent plant characteristics that can have substantial implications for their survival, colonization, growth and mortality. These attributes can not only indicate the response of the plant community to environmental changes (response traits), they can also have a strong influence on the ecosystem function itself (that is, they are effect traits) (Lavorel, et al., 2002). Previous studies on functional traits in ecology are mostly approached either from the perspective of response traits or of effect traits, taken independently (Díaz et al., 2004; Wei et al., 2021a). Lavorel and Garnier (2002) proposed the “response-effect trait” framework based on coupling relationships between response traits and effect traits. The framework can comprehensively explain how environmental conditions filter species based on response traits, leading to specific community assembly. The framework can also reveal how community trait composition influences ecosystem functions. For example, environmental factors play a significant role in shaping the traits of species by exerting selective pressures. These factors act as filters that influence the composition or structure of local communities (e.g. Wei et al., 2020). Consequently, plant communities with distinct or contrasting response-trait profiles, as a result of this filtering process, can impact ecosystem processes through variations in the abundance of ecosystem-effect traits (Suding et al. 2008; Wei et al., 2021a). The response traits, effect traits and “response-effect traits” (i.e. the same traits favored by environmental conditions and influencing ecosystem functions) for a specific ecosystem function can be determined based on this framework. In addition, some environmental factors may directly affect ecosystem functions without regulating effect traits; this process is also taken into account in the “response-effect traits” framework (Suding, et al., 2008). Hence, by integrating response traits and effect traits at the community level, we can establish a mechanistic understanding of community assembly and explore the resulting cascading effects on ecosystem functions (Lavorel and Garnier, 2002; Litchman et al., 2015).

Though the “response-effect traits” framework is increasingly being applied (Garnier et al. 2004; Laliberte and Tylianakis 2012), only a few empirical studies have used this framework to understand the mechanisms of community assembly and ecosystem functioning, in specific ecosystems such as agricultural land, wetlands or grasslands (e.g. García-Palacios, 2013; Robleño 2017; Solé-Senan 2017; Bartomeus et al., 2018; Maclaren et al., 2018; Fu et al., 2020). Empirical work is especially lacking in restored ecosystems (but see Zirbel et al. (2017), who first applied the "response-effect traits" framework to ecological restoration research in a grassland ecosystem). There have been few studies on plantations, which are quite different from other ecosystems (e.g. wetlands, grasslands) or natural forests in terms of their composition, management practices, biodiversity and ecosystem functioning. Specifically, plantations typically comprise monoculture systems that involve the cultivation of a single or a limited number of carefully chosen tree species. These plantations are actively managed with the goal of maximizing tree growth and yield. Whether and to what extent plantations can benefit a certain type of ecosystem functions, such as carbon and nutrient sequestration and cycling, is not fully understood (Montagnini and Nair, 2004; FAO, 2018). While the tree layers are often selected and planted primarily by forest managers, the understory layers colonize the plantation naturally (although understory planting practices also exist) and succeed along with the development of the tree stand (although understory planting practices also exist). Therefore, different plantation types composed of different tree stands and corresponding understory plants might result in diverse impacts on ecosystem functions. Thus, using the "response-effect traits" framework in the context of plantations can help predict the functional composition of plant communities and their impact on ecosystem functioning. This can aid in identifying and predicting the restoration outcomes of different plantations.

Estimating carbon and nutrient stocks in plantations can provide insights into the health and productivity of forest ecosystems, which are key indicators of ecosystem function and useful for evaluating the efficiency of vegetation restoration in degraded forest ecosystems (Melillo et al., 2011). Carbon and nutrient stocks refer to the total amount stored in different components of an forest ecosystem, such as living or dead biomass and soils. These stocks in plant tissues are directly linked to plant photosynthetic capacity and tissue density. For example, plant species with a higher leaf dry-matter content and stem specific density tend to accumulate more carbon and nutrients (e.g. de Bello et al., 2010; Finegan et al., 2015; Smart et al., 2017, yet see contrary findings in Rosenfield et al., 2020). The carbon and nutrient stocks of the soil and litter pools are also largely determined by the traits of the plants that contribute the organic matter to the litter and soil. Plants have differing traits such as photosynthetic rates, growth rates, litter quality, and root exudation rates, all of which affect the quantity and quality of organic matter they contribute to the soil. For example, low trait values for leaf carbon, nitrogen and phosphorus contents exhibit a correlation with resource conservation, promoting the gradual accumulation of carbon, nitrogen or phosphorus stocks in the litter and soil (Freschet et al., 2012; Garcia-Palacios et al., 2013). Plantations can be composed of planted overstory trees and understory vegetation with different functional traits, such as differences in growth rates, photosynthetic capacity or defense ability, which ultimately affect ecosystem carbon and nutrient stocks. However, few, if any, of these traits have been studied in plantations (e.g. Roquer-Beni et al., 2021); they are more commonly included in the study of natural forest ecosystems.

Therefore, the objective of this study was to detect the relationships between plantation type, community traits (at both tree and understory layers) and ecosystem nutrient stocks, based on the “response-effect traits” framework. The ecosystem nutrient stocks studied herein are carbon (C), nitrogen (N) and phosphorus (P) stocks for four pools: tree, understory, litter and soil. Furthermore, we hypothesized that the “response-effect traits” would differ between the overstory and understory strata. We address three questions: 1) How do changes in plantation type influence the functional traits of overstory trees and understory plants, which, in turn, will affect the C, N and P stocks in both the plants themselves and the tree and soil litter? 2) Which tree and understory traits are important "response-effect traits" that can mediate the effects of plantation type on C, N and P stocks? 3) What is the relative importance of the total effect of plantation type and functional traits in explaining C, N and P stocks? The detailed hypotheses on plantation type effects on traits, and plantation and trait effects on C and N stocks are included in the Supplementary Material (SM.1).

2. Materials and Methods

2.1 Research area

The national field research station of Heshan forest ecosystems (HSF, 112°50′ E, 22°40′ N) is situated in the southern region of China, specifically in Guangdong Province. Elevation is less than 100 m and the site is located in a typical southern subtropical monsoon climate. Mean annual temperature was 21 °C and mean annual rainfall was 1948 mm between 2012 and 2021. The distribution of rainfall is uneven, and there is a clear distinction between the wet and dry seasons. Soil conditions are homogeneous; The soil present at the site is laterite, resulting from the weathering process that occurs in the Earth's crust involving granitic rocks (Yu and Peng, 1996). Prior to 1940, the site underwent complete deforestation in order to expand agricultural land, resulting in significant land degradation.

As one of the 40 field stations within the Chinese Ecosystem Research Network (CERN) (Fu et al., 2010), HSF serves as an experimental platform established to understand the long-term effects of forest restoration management on changes in ecosystem patterns and the underlying mechanisms. Specifically, the objective of the experimental design at the station is to establish plantations representing typical plantation types found in subtropical regions. This allows us to understand and predict the potential of these plantations in maintaining biodiversity and ecosystem functioning. To achieve this goal, the station's location was carefully chosen as an ideal site for the experiment. It shares a similar land use history and soil conditions while remaining undisturbed by neighboring villages. Furthermore, since the establishment of the plantations, the management approach strictly adheres to the principle of "natural restoration", meaning that no human intervention was applied (Ren et al., 2007). Consequently, under these conditions, the plantation type represents the only treatment in this study.

In 1984, a total of 26 ha of experimental plantations were established on the barren hilly grasslands, which were previously the site of evergreen broadleaved forests. The fast-growing exotic and native tree species were planted, and no fertilizers were used. We selected three plantation types: an exotic monoculture (*Acacia mangium*), a native conifer mixture (*Pinus massoniana*: *Cunninghamia lanceolata* ≈ 1:1) and a native broad-leaved mixture (*Schima wallichii, Castanopsis hystrix, Michelia macclurei* and *Cinnamomum burmannii,* with a relative mixture ratio of ≈ 3:2:3:2). There are three replicates in each plantation (c.f. similar to Fig. SM.1 in Wei et al. (2021b)), and the aspects of the replicates are consistent: one facing roughly east, one facing south, and one facing west. The plantations are at similar elevations (80 m) and have a similar degree of slope (20 %–30 %) and similar soil pH (3.94–4.35) (See Table SM.1 in Supplementary Material for the mean value of pH for each plantation type). The mean diameter at breast height and mean tree height were 18.4 cm and 12.4 m, respectively, at the time of the study (2019). The mean basal area and canopy cover were respectively 2.14 m^2 ha^{-1} and 71.8 % (for more details on tree stand attributes for each plantation type, see Table SM. 1 in Supplementary Material). Among the tree species planted, *A. mangium* was introduced to Southern China from Australia in 1979 for its nitrogen-fixing, drought-tolerant and fast-growth characteristics (Booth and Yan, 1991). The two native coniferous tree species, *C. lanceolata and P. massoniana*, are widely distributed throughout Central and Southern China. *C. lanceolata* is a pioneer species with rapid growth and excellent wood quality (Tian, 2005); it plays an important role in carbon sequestration and decreasing runoff (Fang et al., 2001). *P. massoniana* exhibits resilience in impoverished and challenging environments and, when employed as a shelter species, can enhance the sustainable utilization of forest lands (Parker, 1982; Xiang et al., 2011). The four native broadleaved tree species are widespread in the subtropical area of Southern China, and are characterized by their high quality wood and high-yield timber production.

2.2 Data collection

2.2.1 Vegetation surveys

Twenty-two 100-m^2 plots were established within each of the three plantation types (66 plots in total). From May to September in 2019, we surveyed and recorded forest vegetation according to plant growth-form and vertical stratum. The stands were divided into two distinct layers: the tree layer, which encompassed vegetation above 7 m in height, and the understory layer, which included vegetation below 7 m in height. In practice, the 7-m threshold effectively distinguished between the planted trees and the naturally-established vegetation. Consequently, the tree layer exclusively comprised the planted trees, each of which was assigned a unique serial number upon planting. The understory layer consisted of herbaceous species (vascular plants including ferns), as well as shrub and small tree species, with the majority of individuals not exceeding a height of 5 m. We took measurements of the diameter at breast height (DBH) and estimated the height of each planted tree in each plot. Furthermore, we determined the crown diameter of each tree to facilitate the calculation of the cover percentage. In the understory layer, all small trees and shrubs above 2 m in height were also recorded in each plot. To survey herbaceous species, dwarf shrub species and saplings less than 2 m in height, we established four subplots (4 m^2) within each plot. Within each subplot, we recorded the height and cover percentage of each species.

2.2.2 Measuring plant traits

For each tree and understory species, we measured six functional traits that are important for plant productivity, nutrient-use efficiency, and carbon and nutrient stocks (Pérez-Harguindeguy et al., 2013). These traits included stem specific density (SSD), leaf dry matter content (LDMC), specific leaf area (SLA), as well as leaf carbon, nitrogen and phosphorus contents (LCC, LNC and LPC). We collected a varying number of healthy and fully expanded leaves (ranging from ten to twenty, depending on leaf size) from five individual plants of each species in each plantation type. Leaf area was determined using an LI-3000C area meter (LI-COR, Lincoln, Nebraska, USA). Subsequently, the leaves were oven-dried at a constant temperature of 65° C for 72 hours until they reached a consistent weight, and their dry weight was recorded. SLA was calculated by dividing leaf area by dry weight, while LDMC was calculated by dividing leaf dry weight by fresh weight (Pérez-Harguindeguy et al., 2013). The dried leaves were then finely ground into powder, and subsequent analysis included the determination of leaf C, N and P contents. LCC was determined with the potassium dichromate-sulfuric acid oxidation method, LNC was determined by the Kjeldahl method, and LPC was determined by molybdenum－antimony colorimetry method (P érez-Harguindeguy et al., 2013). LCC was determined by employing potassium dichromate-sulfuric acid oxidation, while LNC and LPC were determined using colorimetric analysis with an autoanalyzer, following the method described by Pérez-Harguindeguy et al. (2013). For SSD, we collected stem samples from three to ten, depending on life form (tree, shrub or herb), individual plants of each species in each plantation type. For stems with a diameter less than 6 cm, a 10-cm-long section was cut out at approximately one-third of the stem height. For stems with diameters greater than 6 cm, a slice of the trunk was sawed out at approximately 1.3 m in height. We either directly measured the volume of the fresh stem sample with the volume replacement method, or, for very thin stems, indirectly calculated the volume based on the diameter and length of the stem (Cornelissen *et al*., 2003). The samples were then dried in an oven at 80°C for 72 h. The SSD value of a plant was calculated by dividing the oven-dried mass of the plant's stem sample by the volume of the corresponding section when it was still fresh.

2.2.3 Soil sampling

To measure soil physicochemical properties, four soil samples were collected from randomly chosen locations within each 100-m² plot. These soil samples, measuring 5 cm in diameter and 20 cm in depth, were combined to create a single composite soil sample for each plot (Miatto et al., 2016). Meanwhile, to measure soil bulk density (BD), at each point two soil cores were collected with 100-cm^3 metal cylinders: one at 0-10 cm and one at 10-20 cm depth. Measurements were taken for soil pH, soil organic carbon content (OC) and total nitrogen (N) and phosphorus (P) content for every soil core sample. Soil pH was measured using a pH meter at a water-to-soil ratio of 2.5:1.0. The determination of soil OC and N content was carried out using the potassium dichromate method and the Kjeldahl method, while the molybdenum–antimony colorimetric method was used to determine soil P content (Bremner, 2018). For BD, the volume of the metal cylinder used for core sampling was recorded. After sampling, the soil cores were oven-dried at 105 °C for 72h. BD was calculated by dividing the weight of the dried soil (g) by the volume of the metal cylinder (cm^3).

2.2.4 Estimating C, N and P stocks

We used pre-established allometric equations (Fu et al., 2011) specifically developed for the Heshan station. These equations were applied to calculate the biomass of each component (stem, branches, leaves, and roots) of every individual tree and shrub, by utilizing their measured height and DBH. For estimating the biomass of herbaceous plants and litter, we established a 1-m^2 plot within each of the four 4-m^2 subplots per plot. All herbaceous individuals within the 1-m^2 plots were uprooted, and all the litter (including fallen leaves and small twigs) on the forest floor were collected. We oven-dried the harvested herbaceous plants and litter samples for 72 hours at 80 ℃ and weighed them. Then, in each plantation type we collected samples of the other two organs (stems and roots) in addition to leaves, from three mature individual plants for each species. We determined the C, N and P contents of the plant and litter samples using the same method as those for leaves. We multiplied C, N and P contents with biomass of tree, understory and litter respectively, to determine their C and N stocks. Soil OC or N, stocks were calculated as follows:

$$TX = \sum_{i=1}^{2} X_i \times BD_i \times D_i$$

where *TX* denotes the OC, N or P stocks of the soil (Mg ha^{-1}), *i* represents the 0-10 cm and 10-20 cm soil layers combined, BD_i is the soil bulk density of layers *i* (g cm^{-3}), and

D_i is the thickness of layer i (cm). The details of the relative contribution of the four pools - tree, understory, litter and soil - to total C, N and P stocks in the three plantation types are shown in the Supplementary Material (Fig. SM.1 in Supplementary Material).

2.3 Data analysis

Our predictor variables were (Table 1): 1) plantation type: exotic monoculture, native coniferous mix and native broad-leaved mix; and 2) the community weighted mean (CWM) of each trait for both tree and understory layers. To calculate the CWM (community weighted mean) of each trait, we utilized the dbFD function from the FD R package. The calculation involved weighting the traits by the relative abundance of the species.

To explore the relationships between plantation type, CWM of functional traits, and ecosystem nutrient stocks, we employed structural equation models (SEMs). SEMs serve as a valuable tool for comprehending the direct and indirect effects of predictors within complex multivariate systems, as they allow for the integration of various relationships into a single hypothesized network (Grace et al., 2012). To alleviate departure from normality and to allow us to compare multiple predictors and models (Zuur et al., 2010), we log-transformed and standardized all of our numerical positive variables, as recommended in SEM fitting (Grace et al., 2012; Hoyle 2012). To answer Questions 1 and 2, we predicted ecosystem C, N and P stocks of each pool from CWM traits (for each stand layer), plantation type, with a separate model for each pool. For the categorical variable of plantation type, we converted it into an ordered numeric variable by assuming that the plantation type changed from one type to the next: from the exotic monoculture plantation to the native coniferous plantation and then to the native broadleaved plantation. This allows us to assess the differences in CWM of traits and nutrient stocks between the exotic plantation and native plantations. For each pathway, to evaluate the potential improvement in model adequacy by considering spatial autocorrelation, we applied restricted maximum likelihood (REML) GLS models. These models incorporated the spatial coordinates of each plot to account for spatial autocorrelation in the residuals. GLS models were chosen due to the separate blocks assigned to each plantation type. Although the blocks shared similar soil properties, it was possible that factors correlated with spatial location (such as subtle soil variations or historical factors) beyond plantation type could have influenced the response variables (Ludwig et al., 2020). For Question 3, we also calculated the direct, indirect and total effects of the predictors on the response variable (s) via mediator (s). The standardized total effect of each factor was assessed by summing its direct and indirect effects on C, N or P stocks (Zhang and Chen, 2015; Eldridge et al., 2017). We utilized the piecewiseSEM package (Lefcheck, 2016) to implement the SEM modeling. For all our statistical analyses, we used R 4.1.1 (R Core Team, 2021).

Although functional diversity could be considered another aspect of trait indices in addition to the CWM of traits, we did not include it in our study because, within the context of our plantations, the primary objective was to identify potential traits at the community level that could explain the restoration of ecosystem nutrient stocks. To compare the relative importance of functional diversity to CWM of traits, we also constructed SEMs that used functional richness, functional evenness and functional divergence (FRic, FEve, and FDiv) as three functional diversity indices. AIC values indicated that that the original CWM SEMs were better models than SEMs based on functional diversity for all the types of nutrients stocks considered (Table SM. 2 in Supplementary Material). Furthermore, functional diversity in the SEMs only exhibited responses to plantation type and did not show any effect on nutrient stocks for all pools, except for a negative impact of tree FDiv on soil C stocks.

Similarly, to further investigate whether the abundance of dominant tree species can better explain the differences in CWM of traits and nutrient stocks than plantation type itself, we attempted to add two new types of SEMs (see concept diagrams in Fig. SM.2 in Supplementary Material): (1) replacing the plantation type with tree abundance in all SEMs, and (2) adding tree abundance to the original SEMs related to plantation type. In the latter case, tree abundance serves as both the response variable to plantation type and the predictor variable for explaining CWM of traits and nutrient stocks. We then conducted model comparisons based on AIC values among the two types of newly added SEMs and the original SEMs. The AIC values indicated that the original SEMs with plantation type were the best models compared to the two new types of models incorporating tree abundance (Table SM. 3 in Supplementary Material). Furthermore, the SEMs showed that tree abundance could be influenced by plantation type but did not have significant effects on the CWM of both tree and understory traits, and tree abundance only sometimes affected nutrient stocks. Based on these results, we have chosen not to consider the SEMs related to functional diversity or tree abundance.

3. Results

According to the tree layer SEM results (Fig. 1), changing plantation type from exotic monoculture (EM) to native coniferous (NC) (i.e. EM to NC) or to native broad-leaved mix (NB) (i.e. EM to NB) (hereafter “plantation type change”) explained the variation in the community weighted mean (CWM) of all the tree leaf traits other than SSD_{tr}. Specifically, both native plantations had lower SLA_{tr}, LNC_{tr} and LPC_{tr} but higher $LDMC_{tr}$ than the EM; LCC_{tr} in native coniferous mix was higher than in exotic monoculture, but lower in native broad-leaved mix compared to exotic monoculture (see trait values for each plantation type in Table SM. 4 in Supplementary Material). Concerning effects on C and N stocks, tree traits did not show any significant effects on tree C and P stocks themselves, while only SSD_{tr} had a negative relationship with tree N stocks. Since SSD_{tr} did not vary with plantation change, only "effect traits" rather than "response-effect traits" were identified for tree pool N stocks. Besides, plantation type change from EM to NB had a direct positive effect on tree pool C and P stocks.

In the understory layer (Fig. 2, D-F), the change from EM to the two native plantations resulted in a reduced CWM for all trait values, except for the statistically non-significant responses of SLA_{un} and LCC_{un} to the plantation change from NC to EM and of $LDMC_{un}$ and LCC_{un} to the change from EM to NB. LPC_{tr} had a negative effect on understory C and N stocks (Fig. 2, A-C), and SSD_{un} or SLA_{un} had a negative effect on the understory C, N or P stocks(Fig. 2, D-F) Correspondingly, the change of plantation type from EM to NC had an indirect positive impact through its effect on SSD_{un}, and the change of plantation type from EM to NB had an indirect positive impact through its effect on LPC_{tr}, SSD_{un} or SLA_{un}. Therefore, $LPC_{tr,}$ SSD_{un} and SLA_{un} were "response-effect traits" of C, N or P stocks of the understory pool. Besides, the change of plantation type from EM to NB had a direct negative effect on understory C, N and P stocks, and the change of plantation type from EM to NC/NB had direct negative effects on understory C and P stocks.

For factors affecting litter and soil C, N and P stocks (Figs 3&4), both tree and understory traits showed significant effects. Specifically, tree LPC_{tr} had negative effects on litter C and N stocks, and tree LCC_{tr} had significantly negative effects on litter P stocks and soil C, N and P stocks. The understory SLA_{un} and LPC_{un} negatively affected the C and N stocks in the litter pool, while understory LCC_{un} and LNC_{un} negatively affected the C or N stocks in the soil pool. Therefore, plantation type change (EM to

NB/NC) did indeed affect the C, N and P stocks in the litter via LPC_{tr}, LCC_{tr}, SLA_{un} and LPC_{un}, or affected soil pools via LCC_{tr} and LNC_{un}, which are therefore “response-effect” tree traits for those two pools. Accordingly, the change of plantation type from EM to NC/NB had positive indirect impacts on litter C, N and P stocks through tree traits such as LPC_{tr} or LCC_{tr} and understory traits like SLA_{un} and LPC_{un}, as well as positive indirect effects on C, N, or P stocks in the soil pool through its impact on LCC_{tr} or LNC_{un}. Yet, the change from EM to NC had a negative indirect effect on litter P stocks and soil C, N, and P stocks via LCC_{tr}. In addition, the direct negative effect of plantation type change from EM to NC/NB on the C, N and P stocks of the litter pool could also be detected (see the value of C, N, and P stocks for each plantation type in Table SM. 4 in Supplementary Material). For the soil pool, soil C and P stocks directly increased with the change of plantation type from EM to NC/NB, but soil N stocks directly decreased with the change of plantation type from EM to NC/NB. Obviously, similar “response-effect traits” for C and N stocks could be detected in the understory, litter, or soil pool. This might be because the C and N stocks in those three pools are strongly correlated, with $r=0.79$ ($P<0.001$), $r=0.96$ ($P<0.001$), and $r=0.81$ ($P<0.001$), respectively, for the understory, litter, and soil pools. However, for the P stocks, it often showed non-significant correlation with C or N stocks.

Among the total effects (including both indirect and direct effects from the SEM models) of plantation type (Figs. 1-4) and tree/understory traits (Figs. 3-5), the plantation change of EM to NB/NC had a greater effect than tree traits on the C, N and P stocks in the tree pool. On the contrary, in the understory pool, traits such as $LDMC_{un}$, SSD_{un} or LPC_{tr} had the highest effects on C, N and P stocks. In the litter pool, the most significant effects were observed from tree and understory traits, except that plantation type can show higher effect than tree/understory trait for litter P stocks. In the soil pool, the greatest effects were found to be the plantation type, except for soil N stocks. As for the direction of total plantation-type effects, we found that EM to NB showed positive effects on the C, N and P stocks of the tree and soil pools (except for soil N stocks). However, it had negative effects on the C, N and P stocks of the understory and litter pools and the N stocks of the soil pool. On the other hand, the total effect of EM to NC on C, N or P stocks was often negative or marginal, except for its positive effect on understory N stocks and soil C and P stocks.

4. Discussion

As hypothesized (SM.1.1 in Supplementary Material), we found that the change of exotic monoculture plantations to native mixed plantations represented a shift in strategy from relatively fast-growing to slow-growing tree species. This was reflected in the decreased community weighted mean of SLA and leaf nutrient concentrations (LCC, LNC, LPC) and an increased dry-mass investment per leaf area (LDMC) of the tree species (Wright, 2004). However, the tree traits of SSD, SLA and LDMC in our study did not explain the C and P stocks in the tree pool itself as we hypothesized. Similar results were found by Conti et al. (2013); in semi-arid forest ecosystems, they showed that none of the CWM of tree leaf traits explained the variations in carbon storage. Furthermore, our study revealed that only one tree trait, SSD, had a significant effect on tree pool N stocks, even though SSD (also called “wood density” in some studies) has been considered important for explaining plant C stocks. We found a negative effect of SSD on N stocks, contrary to our hypothesis of a positive effect (see SM.1.2 (2) in Supplementary Material). Previous studies had shown mixed effects (positive, negative, or no effect) of plant SSD on C or N stocks (de Bello et al., 2010; Finegan et al., 2015; Mensah et al., 2016; Wu et al., 2017). A low CWM of tree SSD can reflect the dominance of fast-growing species, which accumulate more nitrogen stocks, as shown by Rosenfield et al. (2020) for restoration sites, and other studies (Ruiz-Jaen et al., 2010; Mensah et al., 2016; Wu et al., 2017; Wondimu et al., 2021). Regarding the plantation type change effect on C, N and P stocks of the tree pool, the mixed-broad species can enhance overall performance and achieve over-yieldining through complementarity with niche differentiation or facilitation among individuals (Williams et al., 2017), which promoted the storage of carbon in the tree pool especially for broadleaved tree species (Niu et al., 2009; Warner et al., 2022).

The change of exotic monoculture plantations to native mixed plantations was found to result in a decrease in SLA and leaf nutrient concentrations (e.g. LNC and LPC) for understory traits, as observed in the tree layer (see trait values for each plantation type in Table SM. 4 in Supplementary Material). Similar findings were reported in a previous study, which showed a higher LNC in an exotic fast-growing plantation (*Eucalyptus* plantation) compared to two pine plantations in a subtropical area (De Stefano et al., 2019). Yet, contrary to our results for tree-trait responses and to our hypothesis (SM.1.1 in Supplementary Material), the native broad-leaved mix did not exhibit higher understory LDMC or SSD that could have reflected a conservative life strategy. Instead, we found higher LDMC as well as higher SSD in the understory of the exotic monoculture compared to the native plantations. Therefore, the increase in both leaf nutrient content and tissue or leaf density might suggest that the understory in the exotic plantation is heavily investing in both photosynthesis and structural defense, indicating a balanced growth strategy that is beneficial in potentially less stable or fragile plantations, such as exotic monoculture (Poorter, 2009; Reich et al., 2014). However, the negative impact of understory SSD on C, N and P stocks of the understory pool was comparable to SSD impact in the tree layer; this underscores the importance of considering the potential impact of SSD on N stocks in the plant pool. Meanwhile, we found a negative effect of understory SLA and tree LPC on understory C and N stocks (see SM.1.2 (2) in Supplementary Material). Our results are consistent with Garnier et al. (2004) and Mensah et al. (2016); species with low SLA and LPC often slow-growing species that have the capability to conserve internal resources more efficiently. In addition, we found direct negative effect of plantation type change from exotic to native plantations on the C, N and P stocks in the understory pool. This was consistent with our hypothesis (SM.1.2 (2) in Supplementary Material) and indicated that nitrogen-fixing tree species can also benefit the C and N stocks of the understory pool (Zhang et al., 2011).

For traits influencing C, N and P stocks of the litter and soil pools, our study highlighted the role of several key traits, including the LCC and LPC of both the tree and understory layers, and the SLA and LNC of the understory layer. Meanwhile, tree LCC and LPC, and understory SLA, LNC and LPC, responded significantly to plantation type; they are therefore "response-effect traits" for the litter and soil pools. The C, N and P stocks in the litter and soil depend on the equilibrium between nutrient input resulting from primary productivity and nutrient output through processes such as topsoil decomposition, volatilization, leaching, and erosion (Amundson, 2001). Similar to our hypothesis (see SM.1.2 (2) in Supplementary Material), high values for traits associated with high resource acquisition such as SLA, LCC, LNC and LPC, promote fast carbon and nitrogen accumulation in leaves but also faster litter decomposition, leading to lower litter C, N or P stocks (Freschet et al., 2012; Garcia-Palacios et al., 2013). Alternatively, species characterized by conservative leaf traits exhibiting low SLA, LCC, LNC and LPC are inclined to sequester C or N in the soil. As a consequence, this leads to increased soil C, N or P stocks (Ali et al., 2017; Ottoy et al., 2017; Augusto and Boča, 2022). Previous studies have also shown the important role of SLA and LNC in litter and soil C stocks (Garcia-Palacios et al., 2013; Ottoy et al., 2017; Rosenfield and Muller, 2020). Furthermore, we found a strong decrease in litter C, N or P stocks directly and negatively affected by the change of plantation type from exotic to native plantations. This is consistent with our hypothesis that native plantations would have micro-environmental conditions (e.g. canopy cover or soil conditions) promoting litter decomposition (e.g. higher soil moisture and lower temperatures) so that their litter C and N stocks would be lower than in exotic plantations (Kerdraon et al., 2019) (see SM.1.2 (1) in Supplementary Material). Moreover, exotic nitrogen-fixing tree species in exotic plantations could result in higher soil N stocks than in native plantations. However, higher soil C and P stocks were found in the native plantations.

Our study demonstrated that plantation type, i.e. the change of exotic monoculture to native conifer or broad-leaved mix, was a better predictor of C, N and P stocks in the tree pool, P stocks in the litter pool, and C and P stocks in the soil pool than tree traits. This finding was based on our analysis of the total effects estimated from the Structural Equation Models summarizing the direct and indirect effects of each predictor variable. However, when it comes to predicting the less studied pools in previous studies such as understory C, N and P stocks, understory traits can be more significant than the plantation type effect. Interestingly, our results also showed that for the C, N and P stocks of the litter pool, tree or understory traits can play a more important role than plantation type. Furthermore, converting the exotic monoculture to the native broad-leaved mix tended to have an overall positive effect on on the C, N and P stocks of the tree and soil pools, while converting the exotic monoculture to the native coniferous mix had an overall negative or marginal effect on most C and N stocks, though, in both cases, there were exceptions showing the opposite direction. We also discovered that, for certain pools, the direction of the plantation-type direct effect on C or N stocks was reversed compared to plantation-type total effect. For instance, when converting from exotic monoculture to native broad-leaved mix, the direct effect on understory C and N stocks was negative, but the total effect was positive mediated by understory traits. This indicates that the "response-effect traits" play important mediation roles, which can even reverse the direction of plantation-type effects.

Conclusion

In our study, we applied the "response-effect trait" framework to explain community composition and ecosystem nutrient stocks in a forest restoration context. After approximately 35 years of natural restoration, exotic plantations exhibited different tree and understory community traits from native conifer or broad-leaved plantations. We also found "response-effect" tree and understory traits that were significantly influenced by plantation type which, in turn, impacted the C, N and P stocks of the understory pool, as well as tree and understory traits that were identified as "response-effect traits" for the litter and soil pools. This highlights the important role of traits in mediating the effects of plantation type on non-tree pool C and N stocks. Finally, the total effects results reveal that native plantations do not always promote C and N stocks compared to exotic plantations, and that the levels of C, N and P stocks are dependent on the specific species and mixtures of plants used. However, further study is needed to determine whether stand attributes or soil conditions change over time during the restoration period, possibly affecting the understory differently in the long term.

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CRediT authorship contribution statement

Liping Wei: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Writing - original draft. **Frédéric Gosselin:** Conceptualization, Formal analysis, Methodology, Software, Writing - original draft.

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Table 1: Summary of ecological variables

	Category	Variable	Explanation	Mean/SD
Predictor variable	Plantation type change	EMtoNC	Plantation type change from an exotic monoculture (*Acacia mangium*) plantation (EM) to a native coniferous mix (*Cunninghamia lanceolata* and *Pinus massoniana*) (NC)	-
		EMtoNB	Plantation type change from an exotic monoculture (*Acacia mangium*) plantation (EM) to a native broad-leaved mix (mixed with *Schima wallichi*, *Castanopsis hystrix*, *Michelia macclurei* and *Cinnamomum burmannii*) (NB)	-
	Community weighted mean (CWM) of traits	$\mathrm{SSD}_{\mathrm{tr}}$	CWM of tree stem specific density (g cm^{3})	0.50/0.02
		$\mathrm{SLA}_{\mathrm{tr}}$	CWM of tree specific leaf area (cm^{2} g^{-1})	109.20/14.24
		$\mathrm{LDMC}_{\mathrm{tr}}$	CWM of tree leaf dry matter content (mg g^{-1})	395.66/ 72.09
		$\mathrm{LCC}_{\mathrm{tr}}$	CWM of tree leaf carbon content (g kg^{-1})	494.94/31.84
		$\mathrm{LNC}_{\mathrm{tr}}$	CWM of tree leaf nitrogen content (g kg^{-1})	21.48/5.78
		$\mathrm{LPC}_{\mathrm{tr}}$	CWM of tree leaf phosphorus content (g kg^{-1})	0.81/0.16
		$\mathrm{SSD}_{\mathrm{un}}$	CWM of understory stem specific density (g cm^{3})	0.47/0.12
		$\mathrm{SLA}_{\mathrm{un}}$	CWM of understory specific leaf area (cm^{2} g^{-1})	155.87/20.39
		$\mathrm{LDMC}_{\mathrm{un}}$	CWM of understory leaf dry matter content (mg g^{-1})	345.83/24.68
		$\mathrm{LCC}_{\mathrm{un}}$	CWM of understory leaf carbon content (g kg^{-1})	471.41/26.50
		$\mathrm{LNC}_{\mathrm{un}}$	CWM of understory leaf nitrogen content (g kg^{-1})	29.21/8.75
		$\mathrm{LPC}_{\mathrm{un}}$	CWM of understory leaf phosphorus content (g kg^{-1})	0.89/0.12
Response variable	Nutrients stocks	C stocks	Carbon stocks of tree, understory, litter and soil pools. Here, the soil carbon stocks specifically refer to organic carbon (Mg ha^{-1})	Tree: 66.13/19.00 understory: 3.25/1.35 litter:3.03/1.44 soil: 77.37/9.95
		N stocks	Nitrogen stocks of tree, understory, litter and soil pools (Mg ha^{-1})	tree: 3.08/1.80 understory: 0.12/0.05 litter: 0.08/0.04 soil: 5.26/0.71
		P stocks	Phosphorus stocks of tree, understory, litter and soil pools (Kg ha^{-1})	tree: 679.87/81.84 understory: 39.73/17.11 litter: 12.42/3.98 soil: 835.55/334.20

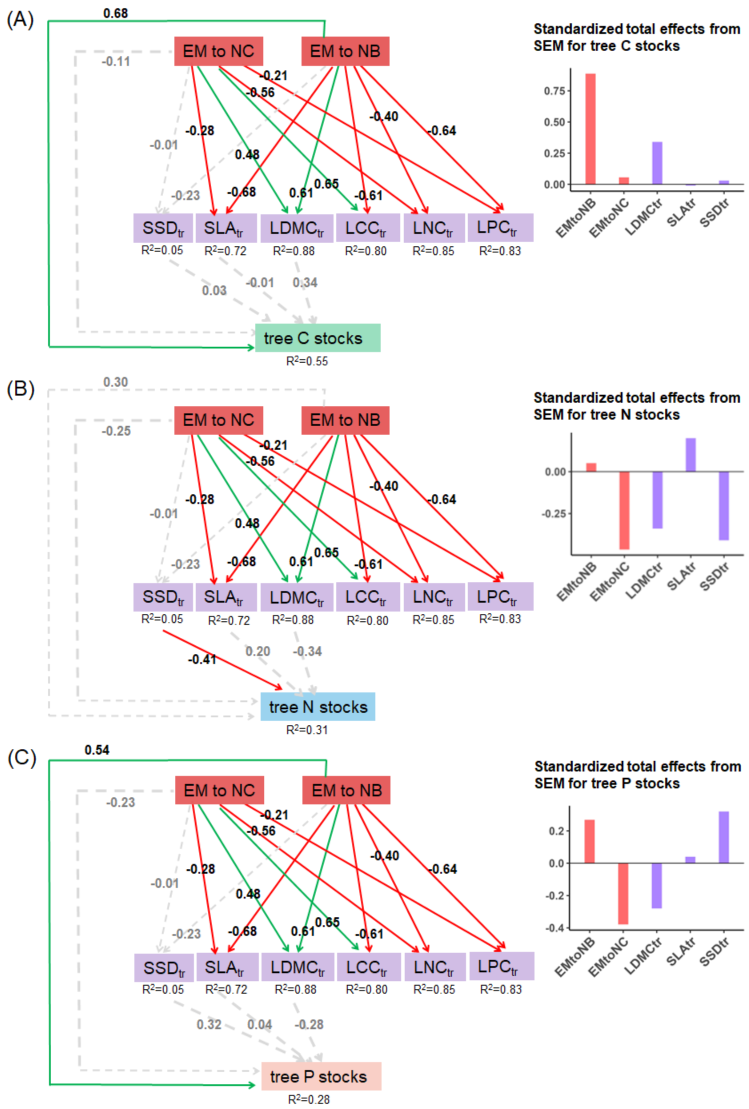

Fig. 1: Structural equation models (SEMs) showing the relationships between plantation type, tree traits and C, N and P stocks for tree pool. The small figures at the top right corner

of each SEM model show the standardized total effect (including direct and indirect effects) of plantation type and functional traits in explaining the relevant C, N or P stocks. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix. Tree traits were SSDtr, SLAtr, LDMCtr, LCCtr, LNCtr and LPCtr. The meanings for the trait abbreviations can be found in Table 1. Solid green arrows represent positive ($P<0.05$) paths and solid red arrows represent negative ($P<0.05$) paths. Dashed grey arrows represent non-significant ($P>0.05$) paths. For each path, the standardized regression coefficient is shown.

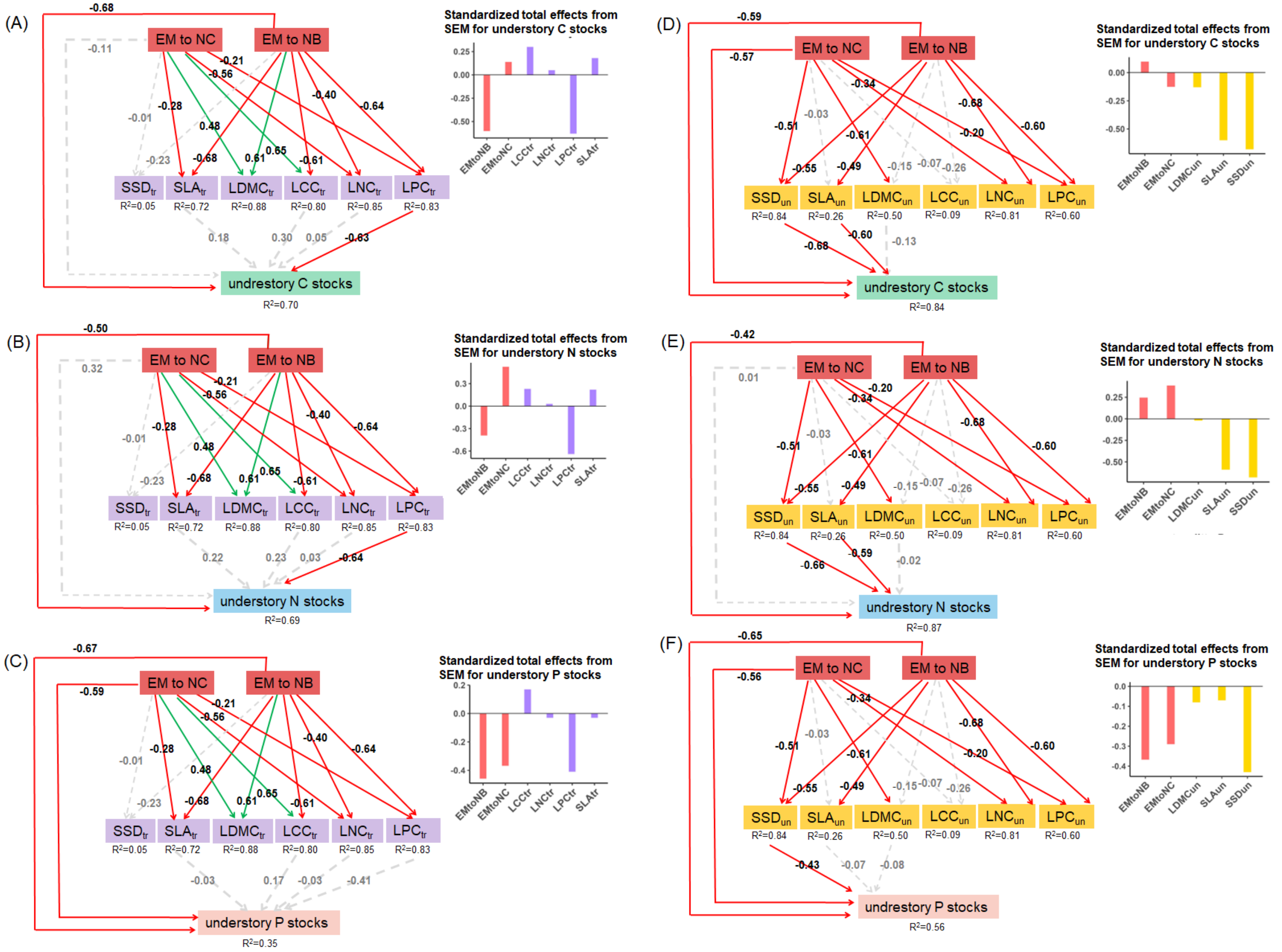

Fig. 2: Structural equation models (SEMs) showing the relationships between plantation type, tree (A-C) or understory (D-F) traits and C (A&D), N (B&E) and P (C&F) stocks for understory pool. The small figures at the top right corner of each SEM model show the standardized total effect (including direct and indirect effects) of plantation type and functional traits in explaining the relevant C, N and P stocks. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix. Tree traits were SSD$_{tr}$, SLA$_{tr}$, LDMC$_{tr}$, LCC$_{tr}$, LNC$_{tr}$ and LPC$_{tr}$. Understory traits

were SSD_{un}, SLA_{un}, $LDMC_{un}$, LCC_{un}, LNC_{un} and LPC_{un}. The meanings for the trait abbreviations can be found in Table 1. Solid green arrows represent positive ($P<0.05$) paths and solid red arrows represent negative ($P<0.05$) paths. Dashed grey arrows represent non-significant ($P>0.05$) paths. For each path, the standardized regression coefficient is shown.

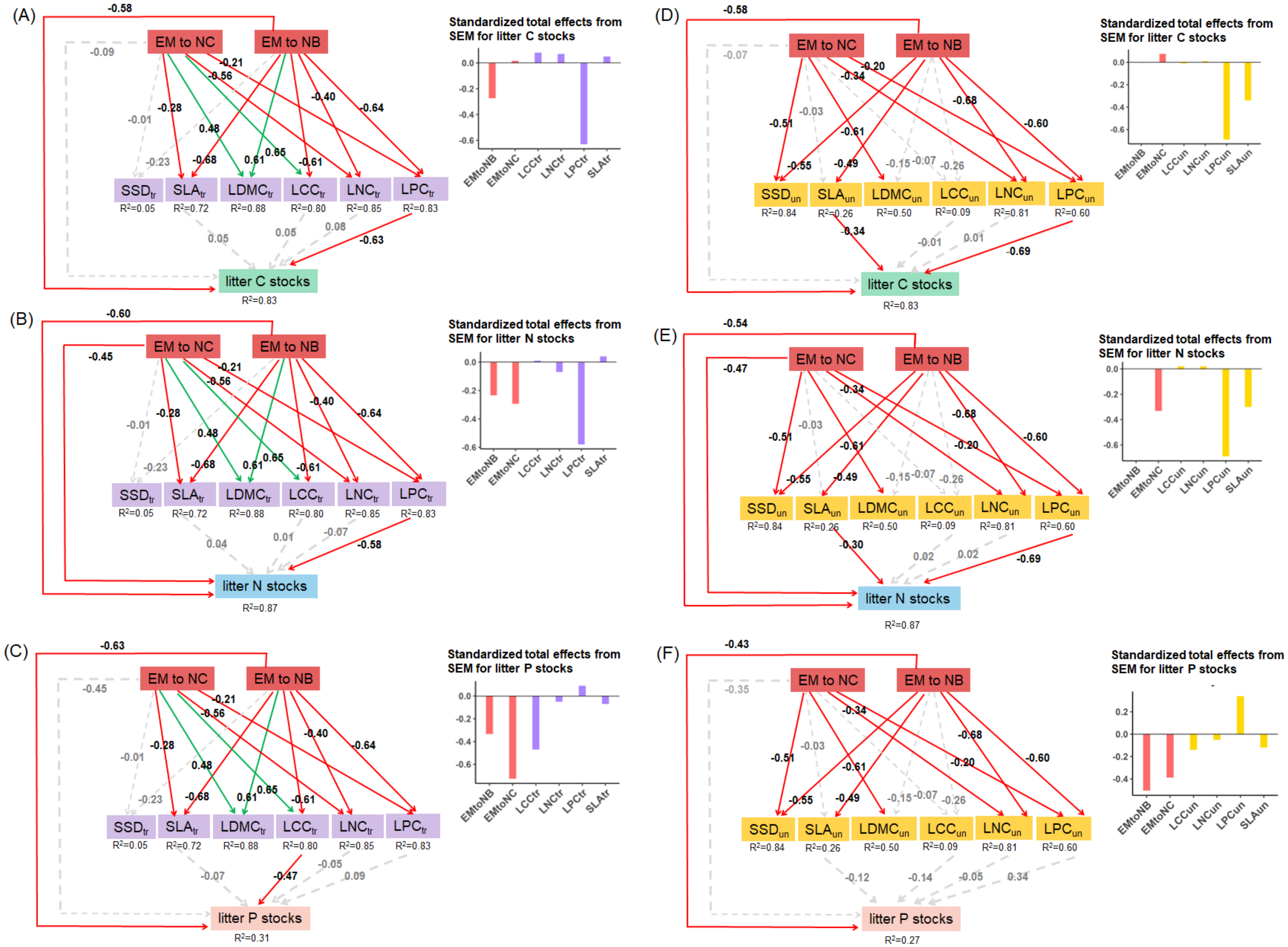

Fig. 3: Structural equation models (SEMs) showing the relationships between plantation type, tree (A-C) or understory (D-F) traits and C (A&D), N (B&E) and P (C&F) stocks for litter pool. The small figures at the top right corner of each SEM model show the standardized total effect (including direct and indirect effects) of plantation type and functional traits in explaining the relevant C, N or P stocks. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix. Tree traits were SSD$_{\mathrm{tr}}$, SLA$_{\mathrm{tr}}$, LDMC$_{\mathrm{tr}}$, LCC$_{\mathrm{tr}}$, LNC$_{\mathrm{tr}}$ and LPC$_{\mathrm{tr}}$. Understory traits were SSD$_{\mathrm{un}}$,

SLA_{un}, LDMC_{un}, LCC_{un}, LNC_{un} and LPC_{un}. The meanings for the trait abbreviations can be found in Table 1. Solid green arrows represent positive ($P<0.05$) paths and solid red arrows represent negative ($P<0.05$) paths. Dashed grey arrows represent non-significant ($P>0.05$) paths. For each path, the standardized regression coefficient is shown.

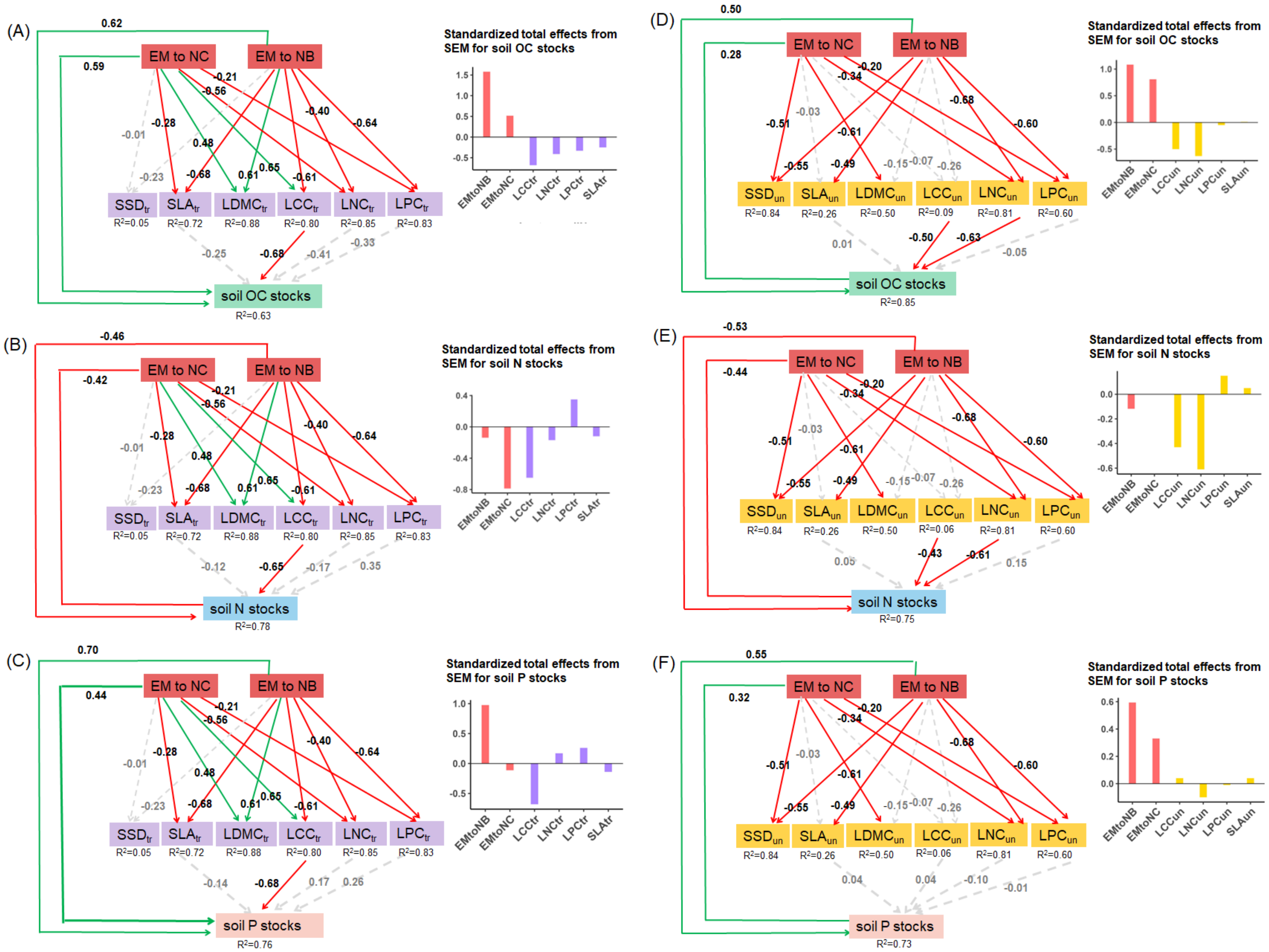
(A)
(B)
(C)
(D)
(E)
(F)
EM to NC
EM to NB
SSDtr
SLAtr
LDMCtr
LCCtr
LNCtr
LPCtr
SSDun
SLAun
LDMCun
LCCun
LNCun
LPCun
soil OC stocks
soil N stocks
soil P stocks
Standardized total effects from SEM for soil OC stocks
Standardized total effects from SEM for soil N stocks
Standardized total effects from SEM for soil P stocks
EMtoNB
EMtoNC
LCCtr
LNCtr
LPCtr
SLAtr
LCCun
LNCun
LPCun
SLAun
0.62
0.59
0.70
0.44
-0.46
-0.42
0.50
0.28
-0.53
-0.44
0.55
0.32
R²=0.63
R²=0.78
R²=0.76
R²=0.85
R²=0.75
R²=0.73

Fig. 4: Structural equation models (SEMs) showing the relationships between plantation type, tree (A-C) or understory (D-F) traits and C (A&D), N (B&E) and P (C&F) stocks for soil pool. The small figures at the top right corner of each SEM model show the standardized total effect (including direct and indirect effects) of plantation type and functional traits in explaining the relevant C, N or P stocks. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix. Tree traits were SSD$_{tr}$, SLA$_{tr}$, LDMC$_{tr}$, LCC$_{tr}$, LNC$_{tr}$ and LPC$_{tr}$. Tree traits were SSD$_{tr}$, SLA$_{tr}$, LDMC$_{tr}$, LCC$_{tr}$, LNC$_{tr}$ and LPC$_{tr}$. Understory traits were SSD$_{un}$, SLA$_{un}$, LDMC$_{un}$, LCC$_{un}$, LNC$_{un}$ and LPC$_{un}$. The meanings for the trait abbreviations can be found in Table 1. Solid green arrows represent positive ($P<0.05$) paths and solid red arrows represent negative ($P<0.05$) paths. Dashed grey arrows represent non-significant ($P>0.05$) paths. For each path, the standardized regression coefficient is shown.

Supplementary Material

SM.1 Theoretical basis for the hypothesized relationships in the structural equation models (EM: exotic monoculture plantation, NC: native coniferous plantation, NB: native broadleaved plantation).

SM.1.1 Plantation type effects on community traits

Plantation type conversion (EM to NC/NB) --------> tree SSD, SLA, LDMC, LCC, LNC and LPC: Though all planted tree species, both exotic and native, are fast-growing species, the exotic species, in particular *Acacia mangium* in our study, are generally considered to have much greater growth rates than native species (Dodet and Collet, 2012). Meanwhile, the exotic species used in forestry plantations can adapt more easily to different environmental conditions and can grow faster in sites with limited soil micro-environmental conditions (such as pH, nutrient availability, moisture content, texture, etc) than can native species. According to the “leaf economics spectrum” by Wright (2004), a fast-growing quick-return species has high leaf nutrient concentrations, high rates of photosynthesis and respiration, and low dry-mass investment per leaf area. We therefore assumed that the exotic tree plantation in our study would have higher community-level SLA, LNC and LPC, and lower LCC, SSD and LDMC than the native tree plantations.

Plantation type conversion (EM to NC/NB) --------> understory SSD, SLA, LDMC, LCC, LNC and LPC: The micro-environment in native plantations, especially native broad-leaved mixtures, should be shadier and more stable than in an exotic monoculture. Therefore, we assumed that the native broad-leaved mixture in our study would be favored by understory indigenous species or conservative species (Aubin et al., 2008; Malysz et al., 2019) with higher LDMC and SSD, and lower LCC, SLA, LNC and LPC (Wright et al., 2004).

SM.1.2 Plantation type and trait effects on ecosystem nutrients stocks

(1) Direct effect of plantation type:

Plantation type (EM to NC/NB) --------> tree carbon, nitrogen and phosphorus stocks: Compared to exotic monoculture plantations, mixed species can enhance overall performance and achive over-yildining through complementarity, with niche differentiation or facilitation among individuals (Williams et al., 2017). which might promote the storage of carbon in the tree pool. However, since trees in exotic monocultures are nitrogen-fixing species and are expected to grow faster, they might have higher N and P stocks than the two native mixed plantations (Mayoral et al., 2017).

Plantation type (EM to NC/NB) --------> understory carbon, nitrogen and phosphorus stocks: Nitrogen-fixing tree species in exotic plantations could maintain a soil with higher available N than in native plantations. This could favor N or P absorption and biomass accumulation by understory species (Zhang et al., 2011). Therefore, we expected higher understory carbon, nitrogen and phosphorus stocks in exotic plantations.

Plantation type (EM to NC/NB) --------> litter and soil carbon, nitrogen and phosphorus stocks: Native plantations are likely to have micro-environmental conditions (e.g. canopy cover or soil conditions) that promote litter decomposition (e.g. higher soil moisture and lower temperatures) and soi microbial activity, so their litter and soil carbon and nutrients stocks should be lower than in exotic plantations (Kerdraon 2019). Meanwhile, Nitrogen-fixing tree species in exotic plantations could result in higher soil N stocks than in native plantations.

(2) Effect of traits:

tree/understory SSD, SLA and LDMC --------> tree/understory carbon, nitrogen and phosphorus stocks: We assumed that tree stands or understory communities with high SSD, SLA and LDMC would have higher carbon and nitrogen stocks. SSD represents the mass per unit volume, which is directly linked to forest carbon sequestration and above-ground biomass (de Bello et al., 2010; Finegan et al, 2015). Plants with a high SLA are associated with high C capture through high photosynthetic N use efficiency. This positively affects above-ground biomass and both carbon and nitrogen stocks (Finegan et al., 2015). LDMC is associated with slower growth rates and is also a good predictor of biomass production and carbon,nitrogen or phosphorus stocks (Smart et al., 2017).

tree/understory SLA, LCC, LNC, LPC --------> litter carbon, nitrogen and phosphorus stock: Traits associated with resource acquisition (high SLA, LCC, LNC and LPC) should promote fast C and N accumulation in the leaves, but even faster litter decomposition. Conversely, lower values for these leaf traits are associated with resource conservation and favor slow carbon, nutrogen and phosphorus accumulation and high stocks (Freschet et al., 2012; Garcia-Palacios et al., 2013)

tree/understory SLA, LCC, LNC, LPC --------> soil carbon, nitrogen and phosphorus stocks: Species with conservative leaf traits (low SLA, LCC, LNC and LPC) are reputed to have the ability to sequester carbon or nitrogen in the soil, thereby enhancing soil carbon, nitrogen and phosphorus stocks (Ali et al., 2017; Ottoy et al., 2017).

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Table SM.1 Mean and SD of tree stand attributes and soil pH for each plantation type

Plantation type	Exotic monoculture	Native coniferous mix	Native broad-leaved mix
DBH (cm)	22.9 ± 6.8	15.5 ± 3.7	17.1 ± 3.0
Height (m)	13.0 ± 3.1	12.3 ± 2.3	12.0 ± 2.0
Canopy cover (%)	71.9 ± 26.7	47.0 ± 20.4	96.4 ± 14.6
Basal area (m^2 ha^{-1})	2.2 ± 1.0	1.7 ± 0.7	2.5 ± 0.9
Soil pH	4.01 ± 0.07	4.19 ± 0.14	4.06 ± 0.10

DBH: tree diameter at breast height (cm).

Table SM. 2 Model comparison between AIC values of SEMs related to community-weighted mean (CWM) of traits and functional diversity (FD)

Nutrient stocks	Trait	delta AIC (CWM.SEM model - FD.SEM model)
tree C stocks	tree	-103.986
tree N stocks	tree	-128.311
litter C stocks	tree	-49.216
litter N stocks	tree	-41.254
soil C stocks	tree	-62.13
soil N stocks	tree	-75.331
understory C stocks	understory	-196.837
understory N stocks	understory	-187.83
litter C stocks	understory	-163.051
litter N stocks	understory	-140.656
soil C stocks	understory	-154.889
soil N stocks	understory	-227.195

Table SM. 3 AIC values of the three types of SEM models shown in Fig. SM.2

Nutrient stocks	Trait	(1) models related to plantation type	(2) models related to tree abundance	(3) model related to plantation type and tree abundance
tree C stocks	tree	730.352	1656.214	859.026
tree N stocks	tree	773.507	1367.526	881.53
tree P stocks	tree	741.158	1228.17	846.119
understory C stocks	tree	1126.999	1914.892	1188.279
understory N stocks	tree	1116.953	1518.229	1179.313
understory P stocks	tree	1094.823	1433.481	1207.59
understory C stocks	understory	732.7	1357.692	854.879
understory N stocks	understory	734.927	975.285	854.033
understory P stocks	understory	717.687	850.55	821.299
litter C stocks	tree	695.259	1329.814	843.106
litter N stocks	tree	682.381	925.966	829.105
litter P stocks	tree	716.462	886.97	781.746
litter C stocks	understory	868.804	1880.416	1122.342
litter N stocks	understory	864.558	1478.932	1096.862
litter P stocks	understory	772.084	1336.033	1285.003
soil C stocks	tree	740.949	1576.025	1078.013
soil N stocks	tree	750.688	1283.081	1080.396
soil P stocks	tree	647.484	991.407	1177.2
soil C stocks	understory	1095.531	2155.078	1163.995
soil N stocks	understory	1128.261	1883.593	1227.703
soil P stocks	understory	1062.9	1620.053	1156.184

Table SM.4 The mean and SD value of varaibles based on plantation type

	Variable	Unit	Exotic monoculture	Native coniferous mix	Native broad-leaved mix
Tree trait	SLA_{tr}	$cm^2 g^{-1}$	122.04±0.09	113.32±6.2	92.44±9.89
	$LDMC_{tr}$	$mg g^{-1}$	298.48±8.14	431.92±17.49	458.22±13.11
	LCC_{tr}	$g kg^{-1}$	493.23±1.66	542.87±8.47	463.59±13.37
	LNC_{tr}	$g kg^{-1}$	29.13±0.44	16.28±3.39	18.06±0.87
	LPC_{tr}	$g kg^{-1}$	0.97±0.01	0.84±0.05	0.61±0.05
	SSD_{tr}	$g cm^3$	0.54±0.03	0.52±0.02	0.47±0.02
Understory trait	SLA_{un}	$cm^2 g^{-1}$	168.18±14.26	154.99±21.97	144.40±17.50
	$LDMC_{un}$	$mg g^{-1}$	368.73±10.07	327.02±18.7	340.87±22.2
	LCC_{un}	$g kg^{-1}$	479.09±30.64	472.15±22.89	463±23.81
	LNC_{un}	$g kg^{-1}$	40.08±4.49	25.15±3.34	22.19±3.25

	LPC$_{un}$	g kg^{-1}	1.02±0.07	0.85±0.06	0.80±0.09
	SSD$_{un}$	g cm^{3}	0.62±0.04	0.39±0.06	0.38±0.03
C stocks	tree C stocks	Mg ha^{-1}	58.14±12.63	53.94±16	85.78±8.63
	understory C stocks	Mg ha^{-1}	4.02±1.37	3.10±0.92	2.64±1.36
	litter C stocks	Mg ha^{-1}	4.43±1.25	2.87±0.78	2.00±0.74
	soil C stocks	Mg ha^{-1}	75.89±8.95	77.86±8.78	77.96±12.16
N stocks	tree N stocks	Mg ha^{-1}	3.17±1.68	2.11±1.67	3.90±1.67
	understory N stocks	Mg ha^{-1}	0.12±0.03	0.13±0.05	0.09±0.06
	litter N stocks	Mg ha^{-1}	0.13±0.04	0.06±0.02	0.05±0.02
	soil N stocks	Mg ha^{-1}	5.48±0.61	5.30±0.90	4.99±0.48
P stocks	tree P stocks	kg ha^{-1}	668.26±73.06	595.50±53.82	775.85±118.64
	understory P stocks	kg ha^{-1}	51.10±20.13	35.45±19.34	32.65±11.85
	litter P stocks	kg ha^{-1}	14.09±4.73	12.99±3.62	10.18±3.59
	soil P stocks	kg ha^{-1}	736.47±310.64	820.37±297.01	949.82±394.95

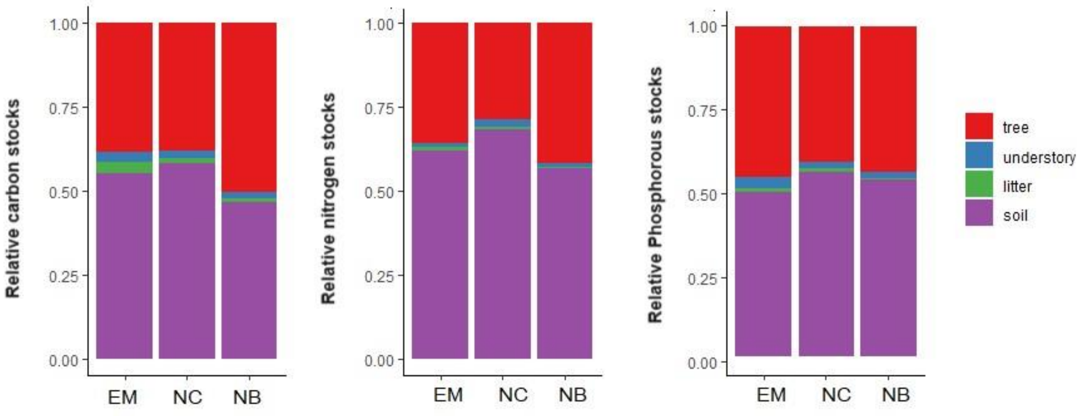

Fig. SM.1: Relative contribution of the four pools - tree, understory, litter and soil to carbon, nitrogen and phosphorus stocks in the three plantation types. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix.

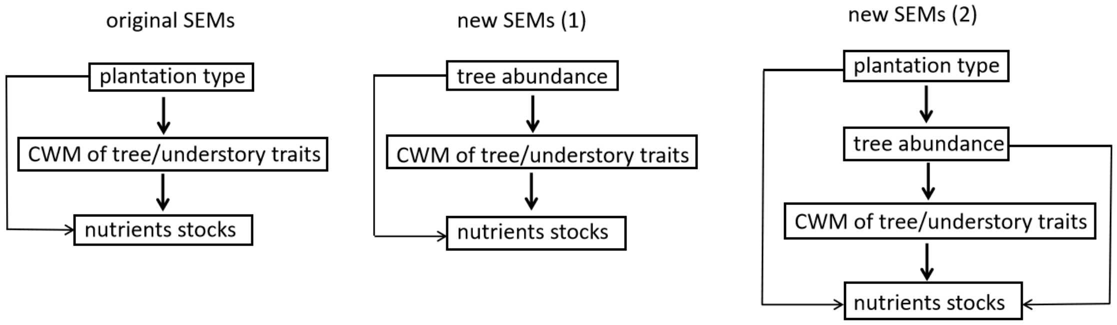

Fig. SM.2 Concept diagrams of SEM models.