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

3

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23 **Abstract**

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

45 restoration, exotic plantations exhibited a different community trait characteristic from  
46 native plantations. The important roles of traits in mediating the effects of plantation  
47 type on non-tree pool C, N and P stocks were highlighted.

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

## 50 **1. Introduction**

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

62 The functional trait-based approaches is valuable for comprehending the processes  
63 of community assembly and ecosystem functions in restoration contexts. Functional  
64 traits represent plant characteristics that can have substantial implications for their  
65 survival, colonization, growth and mortality. These attributes can not only indicate the  
66 response of the plant community to environmental changes (response traits), they can  
67 also have a strong influence on the ecosystem function itself (that is, they are effect  
68 traits) (Lavorel, et al., 2002). Previous studies on functional traits in ecology are mostly

69 approached either from the perspective of response traits or of effect traits, taken  
70 independently (Díaz et al., 2004; Wei et al., 2021a). Lavorel and Garnier (2002)  
71 proposed the “response-effect trait” framework based on coupling relationships  
72 between response traits and effect traits. The framework can comprehensively explain  
73 how environmental conditions filter species based on response traits, leading to specific  
74 community assembly. The framework can also reveal how community trait composition  
75 influences ecosystem functions. For example, environmental factors play a significant  
76 role in shaping the traits of species by exerting selective pressures. These factors act as  
77 filters that influence the composition or structure of local communities (e.g. Wei et al.,  
78 2020). Consequently, plant communities with distinct or contrasting response-trait  
79 profiles, as a result of this filtering process, can impact ecosystem processes through  
80 variations in the abundance of ecosystem-effect traits (Suding et al. 2008; Wei et al.,  
81 2021a). The response traits, effect traits and “response-effect traits” (i.e. the same traits  
82 favored by environmental conditions and influencing ecosystem functions) for a  
83 specific ecosystem function can be determined based on this framework. In addition,  
84 some environmental factors may directly affect ecosystem functions without regulating  
85 effect traits; this process is also taken into account in the “response-effect traits”  
86 framework (Suding, et al., 2008). Hence, by integrating response traits and effect traits  
87 at the community level, we can establish a mechanistic understanding of community  
88 assembly and explore the resulting cascading effects on ecosystem functions (Lavorel  
89 and Garnier, 2002; Litchman et al., 2015).

90        Though the “response-effect traits” framework is increasingly being applied  
91 (Garnier et al. 2004; Laliberte and Tylianakis 2012), only a few empirical studies have  
92 used this framework to understand the mechanisms of community assembly and  
93 ecosystem functioning, in specific ecosystems such as agricultural land, wetlands or

94 grasslands (e.g. García-Palacios, 2013; Robleño 2017; Solé-Senan 2017; Bartomeus et  
95 al., 2018; Maclaren et al., 2018; Fu et al., 2020). Empirical work is especially lacking  
96 in restored ecosystems (but see Zirbel et al. (2017), who first applied the “response-  
97 effect traits” framework to ecological restoration research in a grassland ecosystem).  
98 There have been few studies on plantations, which are quite different from other  
99 ecosystems (e.g. wetlands, grasslands) or natural forests in terms of their composition,  
100 management practices, biodiversity and ecosystem functioning. Specifically,  
101 plantations typically comprise monoculture systems that involve the cultivation of a  
102 single or a limited number of carefully chosen tree species. These plantations are  
103 actively managed with the goal of maximizing tree growth and yield. Whether and to  
104 what extent plantations can benefit a certain type of ecosystem functions, such as carbon  
105 and nutrient sequestration and cycling, is not fully understood (Montagnini and Nair,  
106 2004; FAO, 2018). While the tree layers are often selected and planted primarily by  
107 forest managers, the understory layers colonize the plantation naturally (although  
108 understory planting practices also exist) and succeed along with the development of the  
109 tree stand (although understory planting practices also exist). Therefore, different  
110 plantation types composed of different tree stands and corresponding understory plants  
111 might result in diverse impacts on ecosystem functions. Thus, using the “response-  
112 effect traits” framework in the context of plantations can help predict the functional  
113 composition of plant communities and their impact on ecosystem functioning. This can  
114 aid in identifying and predicting the restoration outcomes of different plantations.

115 Estimating carbon and nutrient stocks in plantations can provide insights into the  
116 health and productivity of forest ecosystems, which are key indicators of ecosystem  
117 function and useful for evaluating the efficiency of vegetation restoration in degraded  
118 forest ecosystems (Melillo et al., 2011). Carbon and nutrient stocks refer to the total

119 amount stored in different components of an forest ecosystem, such as living or dead  
120 biomass and soils. These stocks in plant tissues are directly linked to plant  
121 photosynthetic capacity and tissue density. For example, plant species with a higher leaf  
122 dry-matter content and stem specific density tend to accumulate more carbon and  
123 nutrients (e.g. de Bello et al., 2010; Finegan et al., 2015; Smart et al., 2017, yet see  
124 contrary findings in Rosenfield et al., 2020). The carbon and nutrient stocks of the soil  
125 and litter pools are also largely determined by the traits of the plants that contribute the  
126 organic matter to the litter and soil. Plants have differing traits such as photosynthetic  
127 rates, growth rates, litter quality, and root exudation rates, all of which affect the  
128 quantity and quality of organic matter they contribute to the soil. For example, low trait  
129 values for leaf carbon, nitrogen and phosphorus contents exhibit a correlation with  
130 resource conservation, promoting the gradual accumulation of carbon, nitrogen or  
131 phosphorus stocks in the litter and soil (Freschet et al., 2012; Garcia-Palacios et al.,  
132 2013). Plantations can be composed of planted overstory trees and understory  
133 vegetation with different functional traits, such as differences in growth rates,  
134 photosynthetic capacity or defense ability, which ultimately affect ecosystem carbon  
135 and nutrient stocks. However, few, if any, of these traits have been studied in plantations  
136 (e.g. Roquer-Beni et al., 2021); they are more commonly included in the study of natural  
137 forest ecosystems.

138 Therefore, the objective of this study was to detect the relationships between  
139 plantation type, community traits (at both tree and understory layers) and ecosystem  
140 nutrient stocks, based on the “response-effect traits” framework. The ecosystem  
141 nutrient stocks studied herein are carbon (C), nitrogen (N) and phosphorus (P) stocks  
142 for four pools: tree, understory, litter and soil. Furthermore, we hypothesized that the  
143 “response-effect traits” would differ between the overstory and understory strata. We

144 address three questions: 1) How do changes in plantation type influence the functional  
145 traits of overstory trees and understory plants, which, in turn, will affect the C, N and P  
146 stocks in both the plants themselves and the tree and soil litter? 2) Which tree and  
147 understory traits are important “response-effect traits” that can mediate the effects of  
148 plantation type on C, N and P stocks? 3) What is the relative importance of the total  
149 effect of plantation type and functional traits in explaining C, N and P stocks? The  
150 detailed hypotheses on plantation type effects on traits, and plantation and trait effects  
151 on C and N stocks are included in the Supplementary Material (SM.1).

## 152 **2. Materials and Methods**

### 153 2.1 Research area

154 The national field research station of Heshan forest ecosystems (HSF, 112°50' E,  
155 22°40' N) is situated in the southern region of China, specifically in Guangdong  
156 Province. Elevation is less than 100 m and the site is located in a typical southern  
157 subtropical monsoon climate. Mean annual temperature was 21 °C and mean annual  
158 rainfall was 1948 mm between 2012 and 2021. The distribution of rainfall is uneven,  
159 and there is a clear distinction between the wet and dry seasons. Soil conditions are  
160 homogeneous; The soil present at the site is laterite, resulting from the weathering  
161 process that occurs in the Earth's crust involving granitic rocks (Yu and Peng, 1996).  
162 Prior to 1940, the site underwent complete deforestation in order to expand agricultural  
163 land, resulting in significant land degradation.

164 As one of the 40 field stations within the Chinese Ecosystem Research Network  
165 (CERN) (Fu et al., 2010), HSF serves as an experimental platform established to  
166 understand the long-term effects of forest restoration management on changes in  
167 ecosystem patterns and the underlying mechanisms. Specifically, the objective of the



168 experimental design at the station is to establish plantations representing typical  
169 plantation types found in subtropical regions. This allows us to understand and predict  
170 the potential of these plantations in maintaining biodiversity and ecosystem functioning.  
171 To achieve this goal, the station's location was carefully chosen as an ideal site for the  
172 experiment. It shares a similar land use history and soil conditions while remaining  
173 undisturbed by neighboring villages. Furthermore, since the establishment of the  
174 plantations, the management approach strictly adheres to the principle of "natural  
175 restoration", meaning that no human intervention was applied (Ren et al., 2007).  
176 Consequently, under these conditions, the plantation type represents the only treatment  
177 in this study.

178 In 1984, a total of 26 ha of experimental plantations were established on the barren  
179 hilly grasslands, which were previously the site of evergreen broadleaved forests. The  
180 fast-growing exotic and native tree species were planted, and no fertilizers were used.  
181 We selected three plantation types: an exotic monoculture (*Acacia mangium*), a native  
182 conifer mixture (*Pinus massoniana*: *Cunninghamia lanceolata*  $\approx$  1:1) and a native  
183 broad-leaved mixture (*Schima wallichii*, *Castanopsis hystrix*, *Michelia macclurei* and  
184 *Cinnamomum burmannii*, with a relative mixture ratio of  $\approx$  3:2:3:2). There are three  
185 replicates in each plantation (c.f. similar to Fig. SM.1 in Wei et al. (2021b)), and the  
186 aspects of the replicates are consistent: one facing roughly east, one facing south, and  
187 one facing west. The plantations are at similar elevations (80 m) and have a similar  
188 degree of slope (20 %–30 %) and similar soil pH (3.94–4.35) (See Table SM.1 in  
189 Supplementary Material for the mean value of pH for each plantation type). The mean  
190 diameter at breast height and mean tree height were 18.4 cm and 12.4 m, respectively,  
191 at the time of the study (2019). The mean basal area and canopy cover were respectively  
192  $2.14 \text{ m}^2 \text{ ha}^{-1}$  and 71.8 % (for more details on tree stand attributes for each plantation

193 type, see Table SM. 1 in Supplementary Material). Among the tree species planted, *A.*  
194 *mangium* was introduced to Southern China from Australia in 1979 for its nitrogen-  
195 fixing, drought-tolerant and fast-growth characteristics (Booth and Yan, 1991). The two  
196 native coniferous tree species, *C. lanceolata* and *P. massoniana*, are widely distributed  
197 throughout Central and Southern China. *C. lanceolata* is a pioneer species with rapid  
198 growth and excellent wood quality (Tian, 2005); it plays an important role in carbon  
199 sequestration and decreasing runoff (Fang et al., 2001). *P. massoniana* exhibits  
200 resilience in impoverished and challenging environments and, when employed as a  
201 shelter species, can enhance the sustainable utilization of forest lands (Parker, 1982;  
202 Xiang et al., 2011). The four native broadleaved tree species are widespread in the  
203 subtropical area of Southern China, and are characterized by their high quality wood  
204 and high-yield timber production.

## 205 2.2 Data collection

### 206 2.2.1 Vegetation surveys

207 Twenty-two 100-m<sup>2</sup> plots were established within each of the three plantation  
208 types (66 plots in total). From May to September in 2019, we surveyed and recorded  
209 forest vegetation according to plant growth-form and vertical stratum. The stands were  
210 divided into two distinct layers: the tree layer, which encompassed vegetation above 7  
211 m in height, and the understory layer, which included vegetation below 7 m in height.  
212 In practice, the 7-m threshold effectively distinguished between the planted trees and  
213 the naturally-established vegetation. Consequently, the tree layer exclusively comprised  
214 the planted trees, each of which was assigned a unique serial number upon planting.  
215 The understory layer consisted of herbaceous species (vascular plants including ferns),  
216 as well as shrub and small tree species, with the majority of individuals not exceeding

217 a height of 5 m. We took measurements of the diameter at breast height (DBH) and  
218 estimated the height of each planted tree in each plot. Furthermore, we determined the  
219 crown diameter of each tree to facilitate the calculation of the cover percentage. In the  
220 understory layer, all small trees and shrubs above 2 m in height were also recorded in  
221 each plot. To survey herbaceous species, dwarf shrub species and saplings less than 2  
222 m in height, we established four subplots (4 m<sup>2</sup>) within each plot. Within each subplot,  
223 we recorded the height and cover percentage of each species.

### 224 2.2.2 Measuring plant traits

225 For each tree and understory species, we measured six functional traits that are  
226 important for plant productivity, nutrient-use efficiency, and carbon and nutrient stocks  
227 (Pérez-Harguindeguy et al., 2013). These traits included stem specific density (SSD),  
228 leaf dry matter content (LDMC), specific leaf area (SLA), as well as leaf carbon,  
229 nitrogen and phosphorus contents (LCC, LNC and LPC). We collected a varying  
230 number of healthy and fully expanded leaves (ranging from ten to twenty, depending  
231 on leaf size) from five individual plants of each species in each plantation type. Leaf  
232 area was determined using an LI-3000C area meter (LI-COR, Lincoln, Nebraska, USA).  
233 Subsequently, the leaves were oven-dried at a constant temperature of 65° C for 72  
234 hours until they reached a consistent weight, and their dry weight was recorded. SLA  
235 was calculated by dividing leaf area by dry weight, while LDMC was calculated by  
236 dividing leaf dry weight by fresh weight (Pérez-Harguindeguy et al., 2013). The dried  
237 leaves were then finely ground into powder, and subsequent analysis included the  
238 determination of leaf C, N and P contents. LCC was determined with the potassium  
239 dichromate-sulfuric acid oxidation method, LNC was determined by the Kjeldahl  
240 method, and LPC was determined by molybdenum - antimony colorimetry method (P

241 é rez-Harguindeguy et al., 2013). LCC was determined by employing potassium  
242 dichromate-sulfuric acid oxidation, while LNC and LPC were determined using  
243 colorimetric analysis with an autoanalyzer, following the method described by Pérez-  
244 Harguindeguy et al. (2013). For SSD, we collected stem samples from three to ten,  
245 depending on life form (tree, shrub or herb), individual plants of each species in each  
246 plantation type. For stems with a diameter less than 6 cm, a 10-cm-long section was cut  
247 out at approximately one-third of the stem height. For stems with diameters greater than  
248 6 cm, a slice of the trunk was sawed out at approximately 1.3 m in height. We either  
249 directly measured the volume of the fresh stem sample with the volume replacement  
250 method, or, for very thin stems, indirectly calculated the volume based on the diameter  
251 and length of the stem (Cornelissen *et al.*, 2003). The samples were then dried in an  
252 oven at 80°C for 72 h. The SSD value of a plant was calculated by dividing the oven-  
253 dried mass of the plant's stem sample by the volume of the corresponding section when  
254 it was still fresh.

### 255 2.2.3 Soil sampling

256 To measure soil physicochemical properties, four soil samples were collected from  
257 randomly chosen locations within each 100-m<sup>2</sup> plot. These soil samples, measuring 5  
258 cm in diameter and 20 cm in depth, were combined to create a single composite soil  
259 sample for each plot (Miatto et al., 2016). Meanwhile, to measure soil bulk density  
260 (BD), at each point two soil cores were collected with 100-cm<sup>3</sup> metal cylinders: one at  
261 0-10 cm and one at 10-20 cm depth. Measurements were taken for soil pH, soil organic  
262 carbon content (OC) and total nitrogen (N) and phosphorus (P) content for every soil  
263 core sample. Soil pH was measured using a pH meter at a water-to-soil ratio of 2.5:1.0.  
264 The determination of soil OC and N content was carried out using the potassium

265 dichromate method and the Kjeldahl method, while the molybdenum–antimony  
266 colorimetric method was used to determine soil P content (Bremner, 2018). For BD, the  
267 volume of the metal cylinder used for core sampling was recorded. After sampling, the  
268 soil cores were oven-dried at 105 °C for 72h. BD was calculated by dividing the weight  
269 of the dried soil (g) by the volume of the metal cylinder (cm<sup>3</sup>).

#### 270 2.2.4 Estimating C, N and P stocks

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

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

285  
286 where  $TX$  denotes the OC, N or P stocks of the soil (Mg ha<sup>-1</sup>),  $i$  represents the 0-10 cm  
287 and 10-20 cm soil layers combined,  $BD_i$  is the soil bulk density of layers  $i$  (g cm<sup>-3</sup>), and

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

### 291 2.3 Data analysis

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

298 To explore the relationships between plantation type, CWM of functional traits,  
299 and ecosystem nutrient stocks, we employed structural equation models (SEMs). SEMs  
300 serve as a valuable tool for comprehending the direct and indirect effects of predictors  
301 within complex multivariate systems, as they allow for the integration of various  
302 relationships into a single hypothesized network (Grace et al., 2012). To alleviate  
303 departure from normality and to allow us to compare multiple predictors and models  
304 (Zuur et al., 2010), we log-transformed and standardized all of our numerical positive  
305 variables, as recommended in SEM fitting (Grace et al., 2012; Hoyle 2012). To answer  
306 Questions 1 and 2, we predicted ecosystem C, N and P stocks of each pool from CWM  
307 traits (for each stand layer), plantation type, with a separate model for each pool. For  
308 the categorical variable of plantation type, we converted it into an ordered numeric  
309 variable by assuming that the plantation type changed from one type to the next: from  
310 the exotic monoculture plantation to the native coniferous plantation and then to the  
311 native broadleaved plantation. This allows us to assess the differences in CWM of traits

312 and nutrient stocks between the exotic plantation and native plantations. For each  
313 pathway, to evaluate the potential improvement in model adequacy by considering  
314 spatial autocorrelation, we applied restricted maximum likelihood (REML) GLS  
315 models. These models incorporated the spatial coordinates of each plot to account for  
316 spatial autocorrelation in the residuals. GLS models were chosen due to the separate  
317 blocks assigned to each plantation type. Although the blocks shared similar soil  
318 properties, it was possible that factors correlated with spatial location (such as subtle  
319 soil variations or historical factors) beyond plantation type could have influenced the  
320 response variables (Ludwig et al., 2020). For Question 3, we also calculated the direct,  
321 indirect and total effects of the predictors on the response variable (s) via mediator (s).  
322 The standardized total effect of each factor was assessed by summing its direct and  
323 indirect effects on C, N or P stocks (Zhang and Chen, 2015; Eldridge et al., 2017). We  
324 utilized the piecewiseSEM package (Lefcheck, 2016) to implement the SEM modeling.  
325 For all our statistical analyses, we used R 4.1.1 (R Core Team, 2021).

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

337 except for a negative impact of tree FDiv on soil C stocks.

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

### 353 **3. Results**

354 According to the tree layer SEM results (Fig. 1), changing plantation type from  
355 exotic monoculture (EM) to native coniferous (NC) (i.e. EM to NC) or to native broad-  
356 leaved mix (NB) (i.e. EM to NB) (hereafter “plantation type change”) explained the  
357 variation in the community weighted mean (CWM) of all the tree leaf traits other than  
358  $SSD_{tr}$ . Specifically, both native plantations had lower  $SLA_{tr}$ ,  $LNC_{tr}$  and  $LPC_{tr}$  but higher  
359  $LDMC_{tr}$  than the EM;  $LCC_{tr}$  in native coniferous mix was higher than in exotic  
360 monoculture, but lower in native broad-leaved mix compared to exotic monoculture



361 (see trait values for each plantation type in Table SM. 4 in Supplementary Material).  
362 Concerning effects on C and N stocks, tree traits did not show any significant effects  
363 on tree C and P stocks themselves, while only  $SSD_{tr}$  had a negative relationship with  
364 tree N stocks. Since  $SSD_{tr}$  did not vary with plantation change, only “effect traits” rather  
365 than “response-effect traits” were identified for tree pool N stocks. Besides, plantation  
366 type change from EM to NB had a direct positive effect on tree pool C and P stocks.

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

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

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

404 Among the total effects (including both indirect and direct effects from the SEM  
405 models) of plantation type (Figs. 1-4) and tree/understory traits (Figs. 3-5), the  
406 plantation change of EM to NB/NC had a greater effect than tree traits on the C, N and  
407 P stocks in the tree pool. On the contrary, in the understory pool, traits such as  $LDMC_{un}$ ,  
408  $SSD_{un}$  or  $LPC_{tr}$  had the highest effects on C, N and P stocks. In the litter pool, the most  
409 significant effects were observed from tree and understory traits, except that plantation  
410 type can show higher effect than tree/understory trait for litter P stocks. In the soil pool,

411 the greatest effects were found to be the plantation type, except for soil N stocks. As for  
412 the direction of total plantation-type effects, we found that EM to NB showed positive  
413 effects on the C, N and P stocks of the tree and soil pools (except for soil N stocks).  
414 However, it had negative effects on the C, N and P stocks of the understory and litter  
415 pools and the N stocks of the soil pool. On the other hand, the total effect of EM to NC  
416 on C, N or P stocks was often negative or marginal, except for its positive effect on  
417 understory N stocks and soil C and P stocks.

#### 418 **4. Discussion**

419 As hypothesized (SM.1.1 in Supplementary Material), we found that the change  
420 of exotic monoculture plantations to native mixed plantations represented a shift in  
421 strategy from relatively fast-growing to slow-growing tree species. This was reflected  
422 in the decreased community weighted mean of SLA and leaf nutrient concentrations  
423 (LCC, LNC, LPC) and an increased dry-mass investment per leaf area (LDMC) of the  
424 tree species (Wright, 2004). However, the tree traits of SSD, SLA and LDMC in our  
425 study did not explain the C and P stocks in the tree pool itself as we hypothesized.  
426 Similar results were found by Conti et al. (2013); in semi-arid forest ecosystems, they  
427 showed that none of the CWM of tree leaf traits explained the variations in carbon  
428 storage. Furthermore, our study revealed that only one tree trait, SSD, had a significant  
429 effect on tree pool N stocks, even though SSD (also called “wood density” in some  
430 studies) has been considered important for explaining plant C stocks. We found a  
431 negative effect of SSD on N stocks, contrary to our hypothesis of a positive effect (see  
432 SM.1.2 (2) in Supplementary Material). Previous studies had shown mixed effects  
433 (positive, negative, or no effect) of plant SSD on C or N stocks (de Bello et al., 2010;  
434 Finegan et al., 2015; Mensah et al., 2016; Wu et al., 2017). A low CWM of tree SSD

435 can reflect the dominance of fast-growing species, which accumulate more nitrogen  
436 stocks, as shown by Rosenfield et al. (2020) for restoration sites, and other studies  
437 (Ruiz-Jaen et al., 2010; Mensah et al., 2016; Wu et al., 2017; Wondimu et al., 2021).  
438 Regarding the plantation type change effect on C, N and P stocks of the tree pool, the  
439 mixed-broad species can enhance overall performance and achieve over-yielding  
440 through complementarity with niche differentiation or facilitation among individuals  
441 (Williams et al., 2017), which promoted the storage of carbon in the tree pool especially  
442 for broadleaved tree species (Niu et al., 2009; Warner et al., 2022).

443 The change of exotic monoculture plantations to native mixed plantations was  
444 found to result in a decrease in SLA and leaf nutrient concentrations (e.g. LNC and LPC)  
445 for understory traits, as observed in the tree layer (see trait values for each plantation  
446 type in Table SM. 4 in Supplementary Material). Similar findings were reported in a  
447 previous study, which showed a higher LNC in an exotic fast-growing plantation  
448 (*Eucalyptus* plantation) compared to two pine plantations in a subtropical area (De  
449 Stefano et al., 2019). Yet, contrary to our results for tree-trait responses and to our  
450 hypothesis (SM.1.1 in Supplementary Material), the native broad-leaved mix did not  
451 exhibit higher understory LDMC or SSD that could have reflected a conservative life  
452 strategy. Instead, we found higher LDMC as well as higher SSD in the understory of  
453 the exotic monoculture compared to the native plantations. Therefore, the increase in  
454 both leaf nutrient content and tissue or leaf density might suggest that the understory in  
455 the exotic plantation is heavily investing in both photosynthesis and structural defense,  
456 indicating a balanced growth strategy that is beneficial in potentially less stable or  
457 fragile plantations, such as exotic monoculture (Poorter, 2009; Reich et al., 2014).  
458 However, the negative impact of understory SSD on C, N and P stocks of the understory  
459 pool was comparable to SSD impact in the tree layer; this underscores the importance

460 of considering the potential impact of SSD on N stocks in the plant pool. Meanwhile,  
461 we found a negative effect of understory SLA and tree LPC on understory C and N  
462 stocks (see SM.1.2 (2) in Supplementary Material). Our results are consistent with  
463 Garnier et al. (2004) and Mensah et al. (2016); species with low SLA and LPC often  
464 slow-growing species that have the capability to conserve internal resources more  
465 efficiently. In addition, we found direct negative effect of plantation type change from  
466 exotic to native plantations on the C, N and P stocks in the understory pool. This was  
467 consistent with our hypothesis (SM.1.2 (2) in Supplementary Material) and indicated  
468 that nitrogen-fixing tree species can also benefit the C and N stocks of the understory  
469 pool (Zhang et al., 2011).

470 For traits influencing C, N and P stocks of the litter and soil pools, our study  
471 highlighted the role of several key traits, including the LCC and LPC of both the tree  
472 and understory layers, and the SLA and LNC of the understory layer. Meanwhile, tree  
473 LCC and LPC, and understory SLA, LNC and LPC, responded significantly to  
474 plantation type; they are therefore “response-effect traits” for the litter and soil pools.  
475 The C, N and P stocks in the litter and soil depend on the equilibrium between nutrient  
476 input resulting from primary productivity and nutrient output through processes such  
477 as topsoil decomposition, volatilization, leaching, and erosion (Amundson, 2001).  
478 Similar to our hypothesis (see SM.1.2 (2) in Supplementary Material), high values for  
479 traits associated with high resource acquisition such as SLA, LCC, LNC and LPC,  
480 promote fast carbon and nitrogen accumulation in leaves but also faster litter  
481 decomposition, leading to lower litter C, N or P stocks (Freschet et al., 2012; Garcia-  
482 Palacios et al., 2013). Alternatively, species characterized by conservative leaf traits  
483 exhibiting low SLA, LCC, LNC and LPC are inclined to sequester C or N in the soil.  
484 As a consequence, this leads to increased soil C, N or P stocks (Ali et al., 2017; Ottoy

485 et al., 2017; Augusto and Boča, 2022). Previous studies have also shown the important  
486 role of SLA and LNC in litter and soil C stocks (Garcia-Palacios et al., 2013; Ottoy et  
487 al., 2017; Rosenfield and Muller, 2020). Furthermore, we found a strong decrease in  
488 litter C, N or P stocks directly and negatively affected by the change of plantation type  
489 from exotic to native plantations. This is consistent with our hypothesis that native  
490 plantations would have micro-environmental conditions (e.g. canopy cover or soil  
491 conditions) promoting litter decomposition (e.g. higher soil moisture and lower  
492 temperatures) so that their litter C and N stocks would be lower than in exotic  
493 plantations (Kerdraon et al., 2019) (see SM.1.2 (1) in Supplementary Material).  
494 Moreover, exotic nitrogen-fixing tree species in exotic plantations could result in higher  
495 soil N stocks than in native plantations. However, higher soil C and P stocks were found  
496 in the native plantations.

497 Our study demonstrated that plantation type, i.e. the change of exotic monoculture  
498 to native conifer or broad-leaved mix, was a better predictor of C, N and P stocks in the  
499 tree pool, P stocks in the litter pool, and C and P stocks in the soil pool than tree traits.  
500 This finding was based on our analysis of the total effects estimated from the Structural  
501 Equation Models summarizing the direct and indirect effects of each predictor variable.  
502 However, when it comes to predicting the less studied pools in previous studies such as  
503 understory C, N and P stocks, understory traits can be more significant than the  
504 plantation type effect. Interestingly, our results also showed that for the C, N and P  
505 stocks of the litter pool, tree or understory traits can play a more important role than  
506 plantation type. Furthermore, converting the exotic monoculture to the native broad-  
507 leaved mix tended to have an overall positive effect on on the C, N and P stocks of the  
508 tree and soil pools, while converting the exotic monoculture to the native coniferous  
509 mix had an overall negative or marginal effect on most C and N stocks, though, in both

510 cases, there were exceptions showing the opposite direction. We also discovered that,  
511 for certain pools, the direction of the plantation-type direct effect on C or N stocks was  
512 reversed compared to plantation-type total effect. For instance, when converting from  
513 exotic monoculture to native broad-leaved mix, the direct effect on understory C and N  
514 stocks was negative, but the total effect was positive mediated by understory traits. This  
515 indicates that the “response-effect traits” play important mediation roles, which can  
516 even reverse the direction of plantation-type effects.

## 517 **Conclusion**

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

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538 **CRedit authorship contribution statement**

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

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799 Table 1: Summary of ecological variables

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

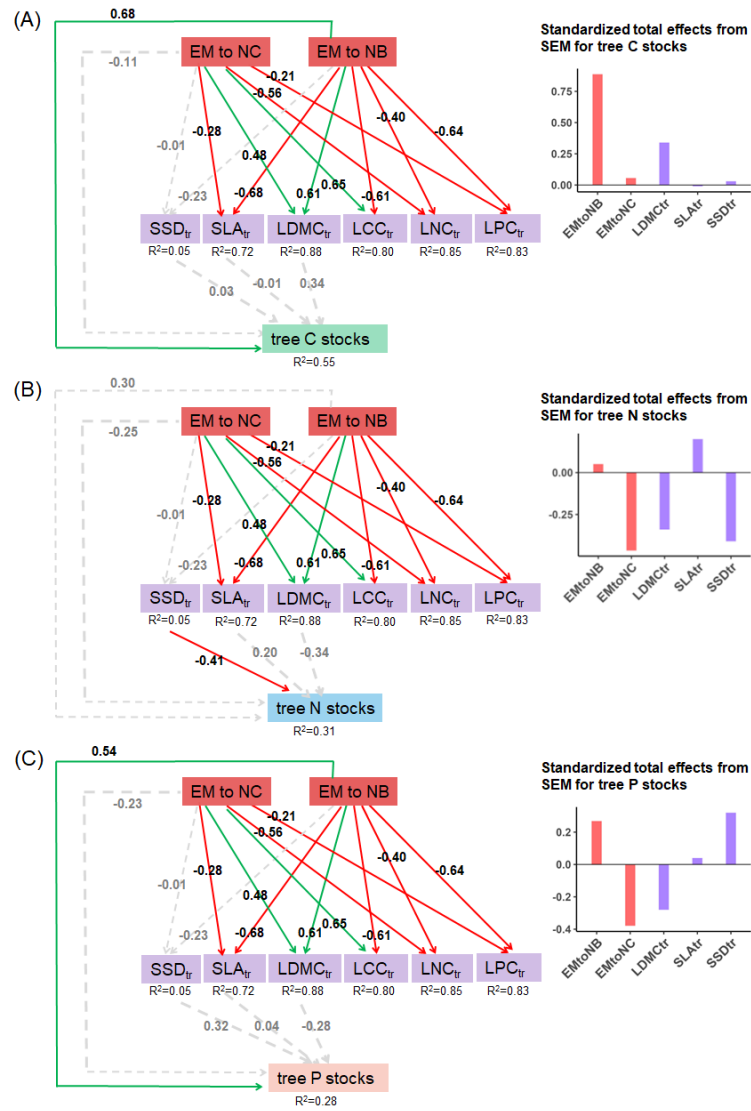
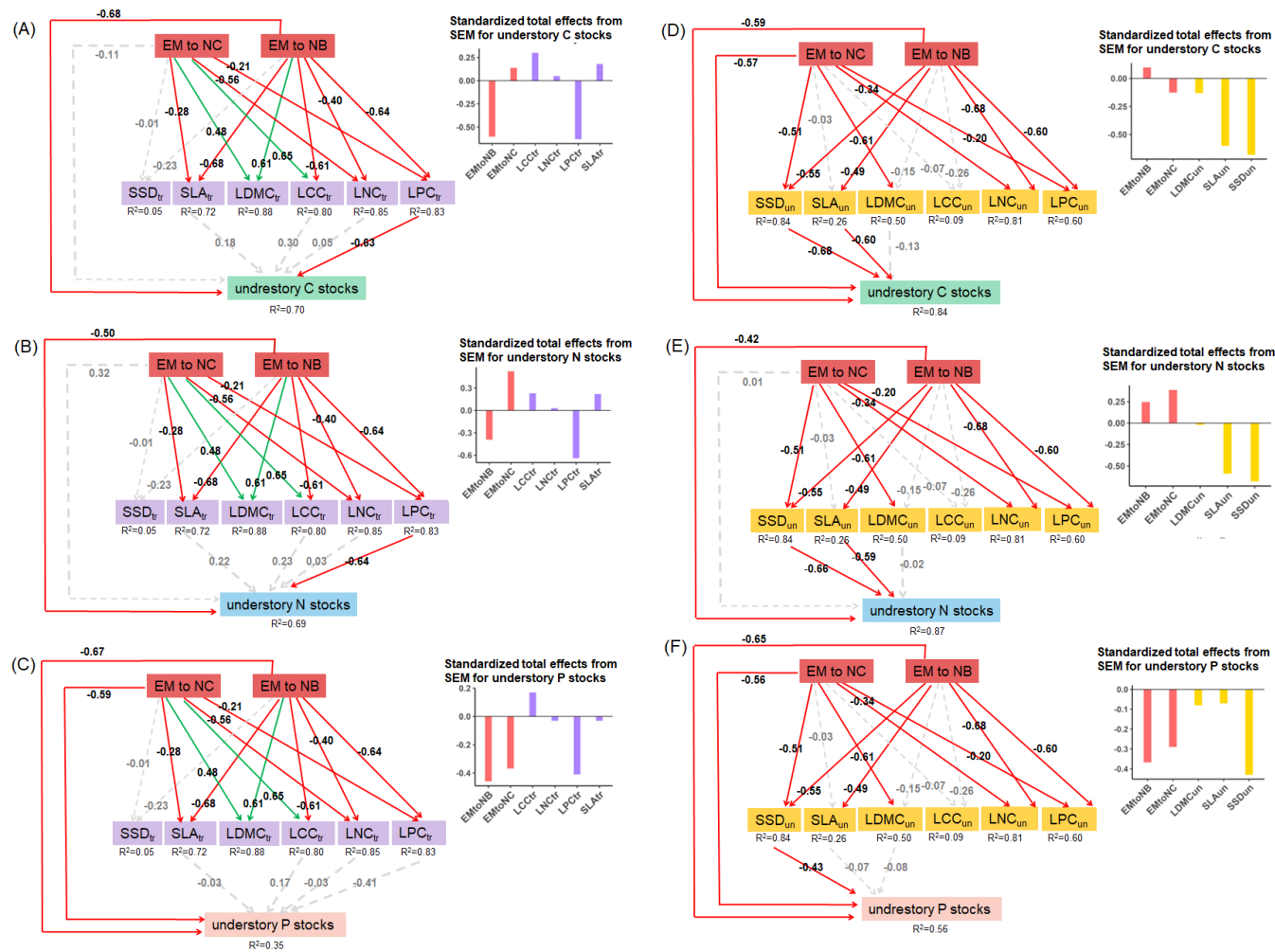


Fig. 1: Structural equation models (SEMs) showing the relationships between plantation type, tree traits and C, N and P stocks for tree pool. The small figures at the top right corner

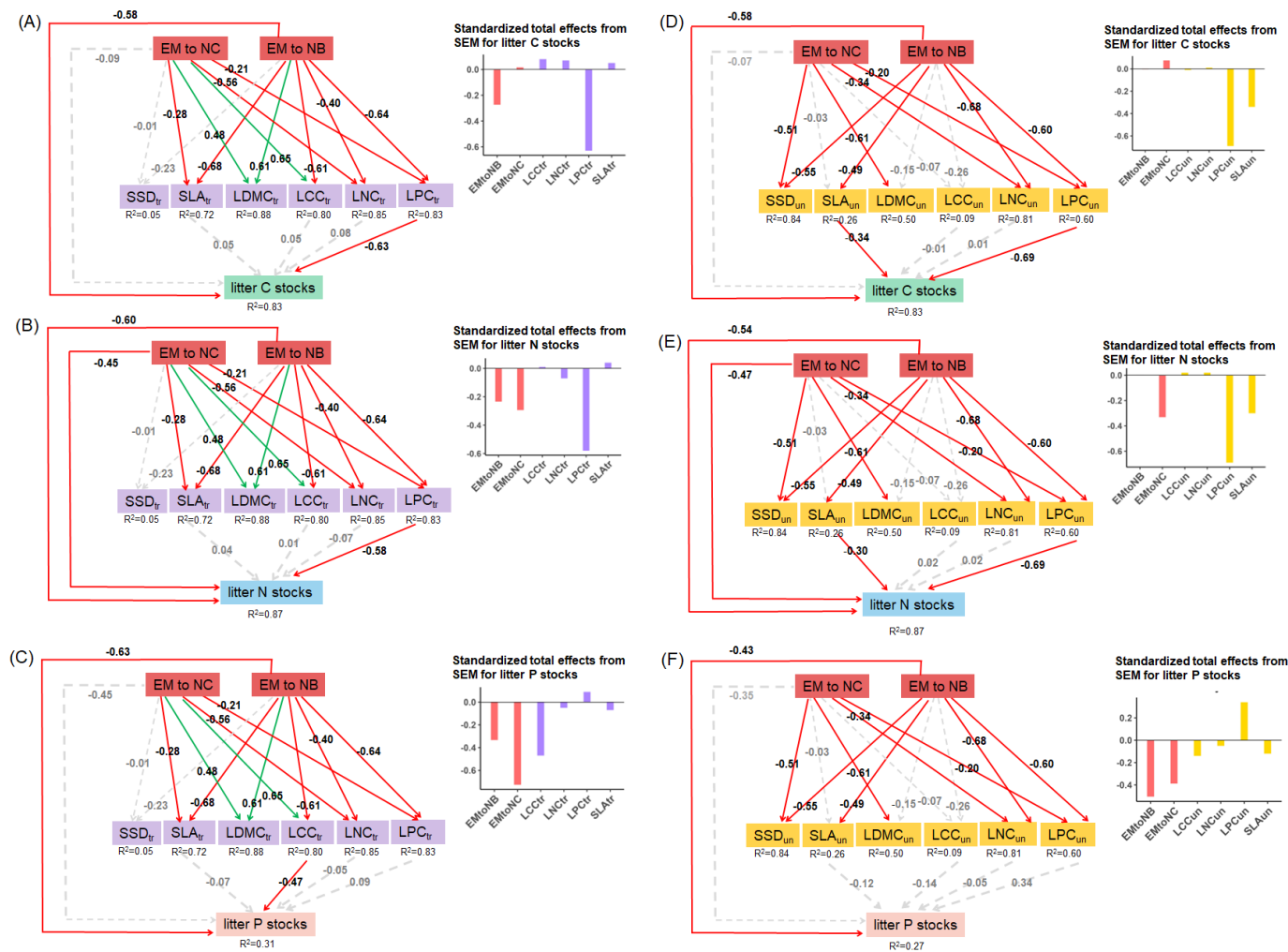
803 of each SEM model show the standardized total effect (including direct and indirect effects) of plantation type and functional traits in explaining the relevant C, N or P stocks. EM:  
804 exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix. Tree traits were SSDtr, SLAtr, LDMCtr, LCCtr, LNCtr and LPCtr. The meanings for the trait  
805 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  
806 non-significant ( $P > 0.05$ ) paths. For each path, the standardized regression coefficient is shown.



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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<sub>tr</sub>, SLA<sub>tr</sub>, LDMC<sub>tr</sub>, LCC<sub>tr</sub>, LNC<sub>tr</sub> and LPC<sub>tr</sub>. Understory traits

811 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  
812 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.  
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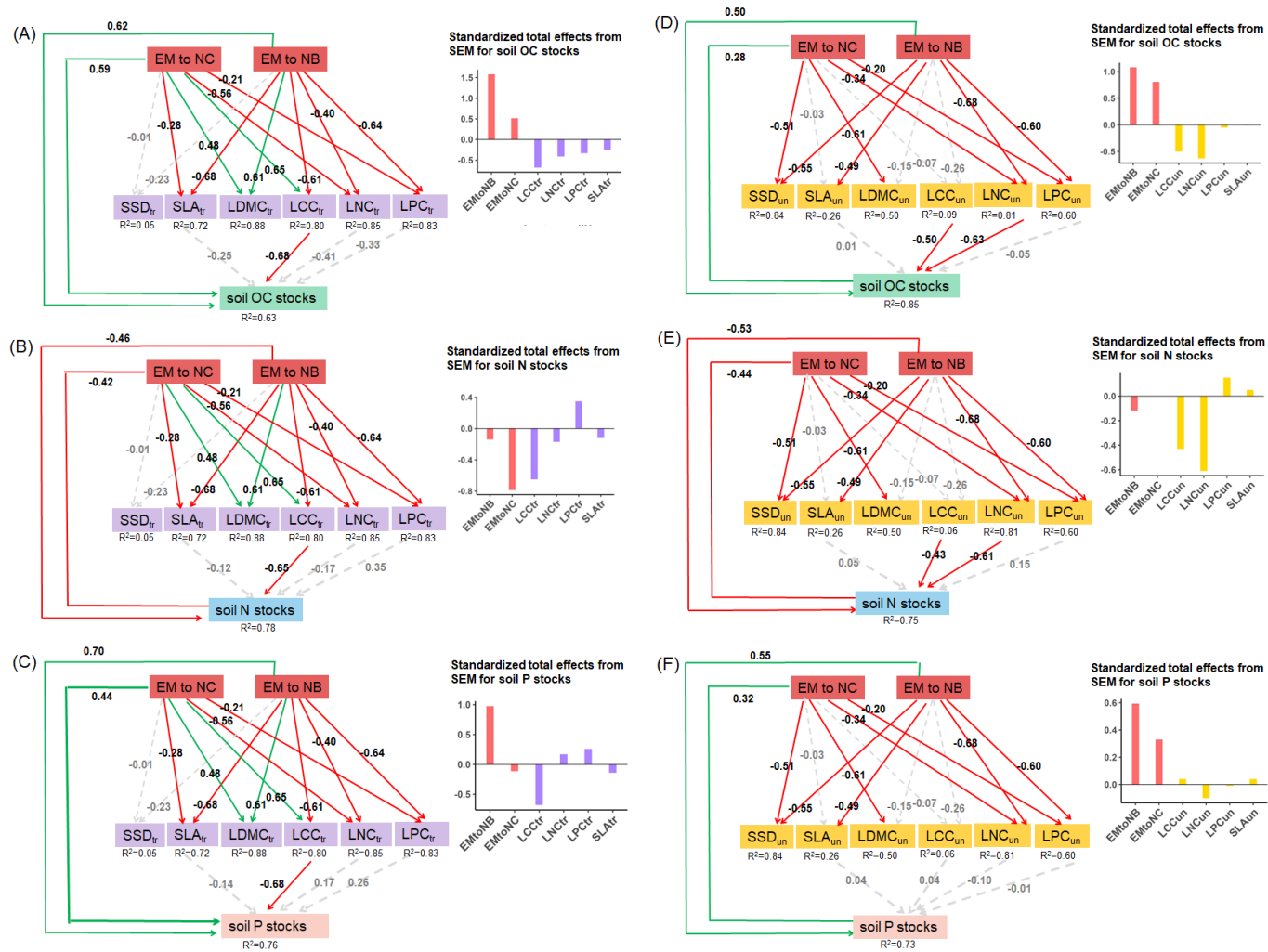
Fig. 3: Structural equation models (SEMs) showing the relationships between plantation type, tree (A-C) or understory (D-F) traits and C (A&D), N (B&E) and P (C&F) stocks for litter pool. The small figures at the top right corner of each SEM model show the standardized total effect (including direct 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<sub>tr</sub>, SLA<sub>tr</sub>, LDMC<sub>tr</sub>, LCC<sub>tr</sub>, LNC<sub>tr</sub> and LPC<sub>tr</sub>. Understory traits were SSD<sub>un</sub>,



818 SLA<sub>un</sub>, LDMC<sub>un</sub>, LCC<sub>un</sub>, LNC<sub>un</sub> and LPC<sub>un</sub>. 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  
819 negative ( $P < 0.05$ ) paths. Dashed grey arrows represent non-significant ( $P > 0.05$ ) paths. For each path, the standardized regression coefficient is shown.

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823 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  
824 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  
825 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  $SSD_{tr}$ ,  $SLA_{tr}$ ,  
826  $LDMC_{tr}$ ,  $LCC_{tr}$ ,  $LNC_{tr}$  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  
827 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  
828 coefficient is shown.

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## 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 achieve over-yielding 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 soil microbial activity, so their litter and soil carbon and nutrients stocks should be lower than in exotic plantations (Kerdran 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, nitrogen 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<br>monoculture | Native<br>coniferous mix | Native broad-<br>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 <sup>2</sup> ha <sup>-1</sup> ) | 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 variables based on plantation type

|                  | Variable           | Unit                            | Exotic<br>monoculture | Native<br>coniferous mix | Native broad-<br>leaved mix |
|------------------|--------------------|---------------------------------|-----------------------|--------------------------|-----------------------------|
| Tree trait       | SLA <sub>tr</sub>  | cm <sup>2</sup> g <sup>-1</sup> | 122.04±0.09           | 113.32±6.2               | 92.44±9.89                  |
|                  | LDMC <sub>tr</sub> | mg g <sup>-1</sup>              | 298.48±8.14           | 431.92±17.49             | 458.22±13.11                |
|                  | LCC <sub>tr</sub>  | g kg <sup>-1</sup>              | 493.23±1.66           | 542.87±8.47              | 463.59±13.37                |
|                  | LNC <sub>tr</sub>  | g kg <sup>-1</sup>              | 29.13±0.44            | 16.28±3.39               | 18.06±0.87                  |
|                  | LPC <sub>tr</sub>  | g kg <sup>-1</sup>              | 0.97±0.01             | 0.84±0.05                | 0.61±0.05                   |
|                  | SSD <sub>tr</sub>  | g cm <sup>3</sup>               | 0.54±0.03             | 0.52±0.02                | 0.47±0.02                   |
| Understory trait | SLA <sub>un</sub>  | cm <sup>2</sup> g <sup>-1</sup> | 168.18±14.26          | 154.99±21.97             | 144.40±17.50                |
|                  | LDMC <sub>un</sub> | mg g <sup>-1</sup>              | 368.73±10.07          | 327.02±18.7              | 340.87±22.2                 |
|                  | LCC <sub>un</sub>  | g kg <sup>-1</sup>              | 479.09±30.64          | 472.15±22.89             | 463±23.81                   |
|                  | LNC <sub>un</sub>  | g kg <sup>-1</sup>              | 40.08±4.49            | 25.15±3.34               | 22.19±3.25                  |

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

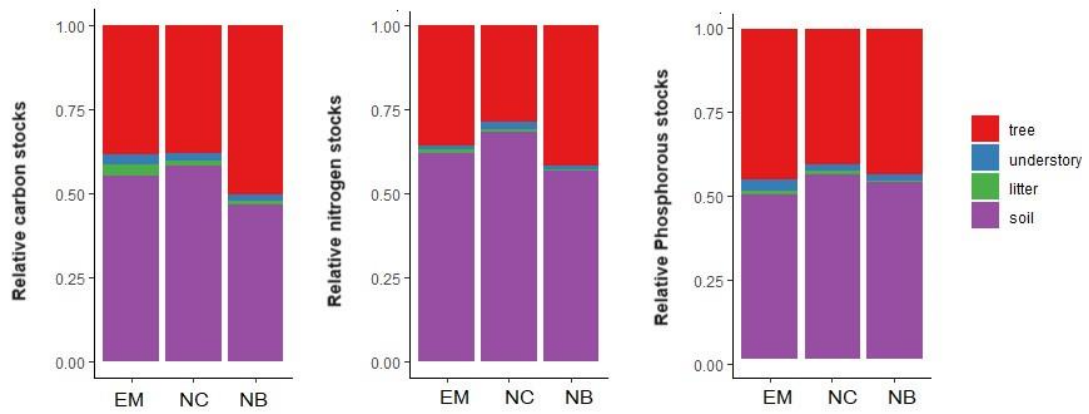


Fig. SM.1: Relative contribution of the four pools - tree, understory, litter and soil to carbon, nitrogen and phosphorus stocks in the three plantation types. EM: exotic monoculture, NC: native coniferous mix, NB: native broad-leaved mix.

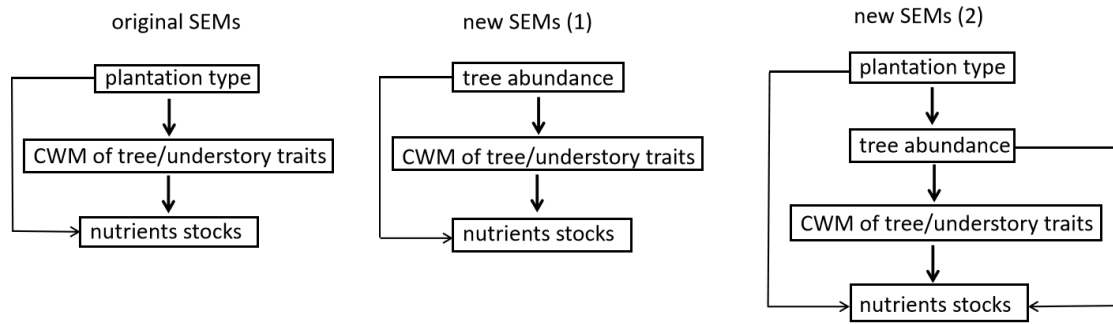


Fig. SM.2 Concept diagrams of SEM models.