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Linking Forest Management Practices to the Functional Composition of Plant Communities

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Abstract: The functional composition of plant communities (FCPC) makes a significant contribution to ecosystem properties, functions, and services. Here, we used 18 plant functional traits from the sPlot database v2.1 and the global forest management type dataset to explore the links between forest management and the FCPC. We used the post hoc Tukey test to explore the differences in the community-weighted mean (CWM) and community-weighted variance (CWV) among different forest management types [i.e., intact forests, managed forests with natural regeneration, planted forests, plantation forests (with up to a 15-year rotation), and agroforestry]. We found that different forest management types can result in significant variability in plant communities' functional composition. Plantation forests could result in significantly higher CWM and CWV compared to intact forests, and significant differences could occur between natural and managed forests with natural regeneration. Furthermore, the relationship between forest management practices and the FCPC depends on ecozone type changes. There were significant differences between natural and plantation forests for CWM and CWV in temperate forests. Our study provides an effective reference for applying plant functional traits to regulate and optimize the functions and services of forest ecosystems.

Keywords: community-weighted mean; community-weighted variance; ecosystem functions; ecozone; plant functional traits; plantation forests

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1. Introduction

The functional composition of plant communities (FCPC) is directly related to ecosystem functions and services, as demonstrated in previous studies for different forest management practices, i.e., natural and plantation forests [1–5]. However, the mechanisms underlying the different forest management practices that affect and shape the FCPC are unclear. Forecasting the two major components of functional composition (i.e., community-weighted mean and variance) is essential for ecosystem management to maximize the benefits for society and the environment [6–8]. Numerous studies have shown that the plant communities' geographic variation in functional composition can be shaped by environmental factors (e.g., climate, soil, and vegetation), which supports a systematic ecosystem properties and functions assessment that will be used to inform policy or for the design of conservation planning or ecological restoration strategies [1,2,4,6,9]. Although previous relevant studies [1–4] have revealed various mechanisms affecting ecosystem functions and services, their role in relation to the environmental management and the FCPC should be studied deeply.

Knowledge of forest management on a global scale is critical for informing policies and decision making, contributing to the improvement in forest management effectiveness, renewable energy, potential supply assessment of forest biomass, carbon sequestration, and ecological restoration practices [10–13]. The FCPC is an effective indicator of ecosystem properties, functions, and services that can support and guide forest management practices [14–16]. Hua et al. (2022) have demonstrated that forest plantations are being scaled-up globally to deliver critical ecosystem services and biodiversity benefits [12]. Ecosystem services, including carbon storage, water provisioning, and especially soil erosion control and biodiversity maintenance, are all better delivered by native forests [12]. Plantations are advantageous for industrial timber harvesting [12]. Le Provost et al. (2020) have demonstrated that land-use history impacts the functional diversity of plant species [17]. Therefore, land use history may be one of the predictors of variation in the FCPC under different forest management types and practices.

The main objective of our study was to explore the relationships between forest management types and practices and the FCPC. Specifically, we aimed to test the following hypotheses:

(1) As previously shown, different forest management types can determine various ecosystem functions and services driven by plant functional traits [5,12]. For example, wood production is closely associated with stem conduit density and wood vessel element length in tree species [18,19]. Here, we propose the first hypothesis (H1): different forest management types can contribute to the variation in the FCPC.

(2) An ecozone is a biogeographical unit consisting of a biological community formed in response to environmental change [20–22]. Ecozone-level relationships may exist between forest management types and ecosystem functions. Here, we propose the second hypothesis (H2): the effects of historical woodland changes on contemporary plant functional diversity vary among different forest ecozones. Different forest ecozones are meant to regulate the relationship between forest management and the FCPC.

Here, we used a linear mixed regression model to investigate the association of plant functional composition (i.e., community-weighted mean (CWM) and community-weighted variance (CWV)), based on 18 plant functional traits from the sPlot database, with five forest management types [23]. The CWM reflects the locally ‘optimal’ trait strategy given a site’s regional species pool and environmental conditions [24]. The CWV indicates different diverse aspects of the ecological strategies and corresponds to the average deviation of individuals from the optimal strategy [25]. Hence, these two indicators of plant functional composition are closely related to ecosystem functions and services under different forest management types. Finally, we propose actionable suggestions on forest management for promoting ecosystem functions and services from the perspective of functional composition.

2. Materials and Methods

2.1. Data on Plant Functional Composition

Analyses were performed based on the 18 plant functional traits that are most closely associated with ecosystem functions and services: (a) leaf area (mm^2); (b) stem-specific density (g/cm^3); (c) specific leaf area (m^2/kg); (d) leaf carbon concentration (mg/g); (e) leaf nitrogen (N) concentration (mg/g); (f) leaf phosphorus (P) concentration (mg/g); (g) mean plant height (m); (h) seed mass (mg); (i) seed length (mm); (j) leaf dry matter content (g/g); (k) leaf N per area unit (g/m^2); (l) leaf N:P ratio (g/g); (m) leaf δ15N (per million); (n) seed number per reproductive unit; (o) fresh leaf mass (g); (p) stem conduit density (per mm^2); (q) dispersal unit length (mm); and (r) wood vessel element length (μm); all measurements were based on the dry weight [23].

We retrieved data on plant functional traits from the sPlot database v2.1 [23]. This database contains 1,121,244 unique vegetation plots and 23,586,216 species records originating from different vegetation plot datasets at regional, national, or continental scales, stemming from regional or continental initiatives [23]. The metadata of each individual vegetation plot dataset stored in the sPlot were managed through the Global Index of Vegetation-Plot Databases (GIVD) [26]. Most of the sPlot database v2.1 data corresponds to natural and seminatural vegetation. In contrast, vegetation shaped by intensive and repeated human interference, such as cropland or ruderal communities, is hardly represented. We performed a natural log transformation of the functional trait data before calculating the CWM and CWV, which indicate intra- and interspecific trait variations regarding plant species composition [27]. The functional trait information was available for 21,854 species across all plots in order to quantify the CWM and CWV of the 18 functional traits evaluated in our study. CWM and CWV were calculated for every plant functional trait j and every vegetation plot k as follows [23]:

$$CWM_{j,k} = \sum_{a}^{n_k} p_{a,k} t_{a,j}$$

$$CWV_{j,k} = \sum_{a}^{n_k} p_{a,k} (t_{a,j} - CWM_{j,k})^2$$

where n_k is the number of species with trait information in vegetation plot k, $p_{a,k}$ is the relative abundance of species a in vegetation plot k calculated as the species' fraction in cover or abundance of total cover or abundance, and $t_{a,j}$ is the mean value of species a for trait j. The range of variation in the proportion of herbaceous (understory) vegetation was based on the species' fraction in cover or abundance of total cover or abundance. Data on lichens and mosses were not considered due to request from the respective dataset custodian or sPlot coordinator.

Finally, 35,283 plots belonging to forest ecozones had enough functional trait information on more than half of the species present in each corresponding plot and were used in our study. The distribution map of the plots used in our study is shown in Figure 1.

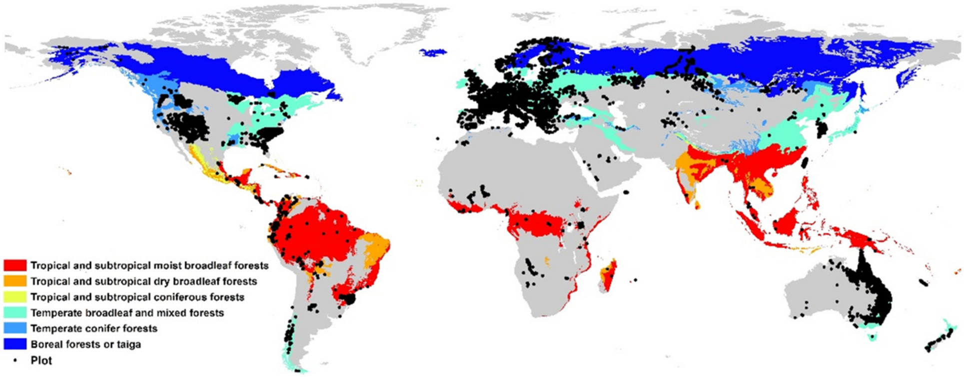

Figure 1. Worldwide distribution of the study plots for CWM and CWV across six forest ecozones.

2.2. Data on Forest Management Types

We obtained the data on forest management types from the study of Lesiv et al. (2022) [13]. This study generated the first reference dataset and a prototype of a globally consistent forest management map with great spatial detail on the most prevalent forest management classes, including intact forests, managed forests with natural regeneration, planted forests, plantation forests (with up to a 15-year rotation), and agroforestry [13]. It is a grid-cell global forest management map at a 100 m resolution for the year 2015 [13]. We focused on the forest ecozones to improve forest management data. Plants belonging to various ecozones on a global scale have different abilities to tolerate anthropogenic transformation of land use [20,21]. Hence, ecozone-level relationships may exist between forest management types and plant functional composition. The forest ecozone types in each of the grid cells used in our study were determined using data from Dinerstein et al. (2017) [21]. The forest ecozones include tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, temperate broadleaf and mixed forests, temperate coniferous forests, and boreal forests/taiga. Thus, we could associate the CWM and CWV plot data with the forest management types across different forest ecozones.

2.3. Analyses

The values of the 18 functional traits were transformed using the natural logarithm and then spatially projected using principal component analysis (PCA). We used PCA to quantify the dimensions of the plant functional traits economics spectrum based on their CWM and CWV, respectively. Based on the study by Joswig et al. (2021) [28], we used PCA to quantify the significant contributors to the primary component of plant functional diversity using CWM and CWV, respectively, with the 18 functional traits used as input. We extracted the respective loadings of the first three principal components (PCs) explaining 66.707% of the variance in CWM and the first five PCs explaining 62.788% of the variance in CWV, which was significant based on the number of axes estimated using a sequential Bonferroni procedure. We assessed the FCPC using the first three CWM-PCs (i.e., three dimensions) and the first five CWV-PCs (i.e., five dimensions).

To test H1, we used the post hoc Tukey test to explore the differences between three CWM-PCs and five CWV-PCs among different forest management types [i.e., intact forests, managed forests with natural regeneration, planted forests, plantation forests (rotation of up to 15 years), and agroforestry] [12]. To test H2, we calculated a response ratio (RR) [plantation forests (i.e., planted forests and agroforestry) over natural forests (i.e., intact forests and managed forests with natural regeneration)] for three CWM-PCs and five CWV-PCs, respectively [12]. We, thus, performed an ANOVA test for each data pair to evaluate differences in the relative performance of plantation forests versus intact forests based on the six forest ecozones, including tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, temperate broadleaf and mixed forests, temperate coniferous forests, and boreal forests/taiga, respectively [21]. All analyses were conducted using the packages “FactoMineR”, “agricolae”, and “ggplot2” in the R environment (https://www.r-project.org/; assessed on 16 March 2023).

3. Results

Based on the loading matrix of PCA as shown as Table 1, CWM-PC1 was positively associated with mean plant height, seed mass, and seed length; CWM-PC2 was positively associated with specific leaf area and leaf nitrogen content per leaf dry mass; and CWM-PC3 was positively associated with leaf phosphorus concentration and dispersal unit length (Table 1). CWV-PC1 was positively associated with leaf area, specific leaf area, leaf N per area unit, and mean plant height; CWV-PC2 was positively associated with seed mass and seed length; CWV-PC3 was positively associated with leaf phosphorus concentration and the leaf N:P ratio; CWV-PC4 was negatively associated with leaf fresh mass; and CWV-PC5 was negatively associated with leaf dry matter content and wood vessel element length. Thus, we used the first three CWM-PCs and the five CWV-PCs for further analyses, as shown in Table 1.

We found significant differences in the three CWM-PCs and five CWV-PCs among the five different forest management types (Figure 2). Overall, plantation forests had significantly higher CWM and CWV than intact forests. With regard to the intact forests, there were significant differences between natural and managed forests with natural regeneration (Figure 2). CWM-PC1, CWV-PC2, CWV-PC3, and CWV-PC4 were significantly higher for intact forests than managed forests with natural regeneration (Figure 2). The differences in CWV were small across plantation forests (rotation $\leq$ 15 years), planted forests (rotation > 15 years), and agroforestry. Plantation forests (rotation $\leq$ 15 years), agroforestry, and planted forests (rotation > 15 years) had the highest CWM-PC1, CWM-PC2, and CWM-PC3 values, respectively (Figure 2). Planted forests (rotation > 15 years) resulted in the highest levels of CWV-PC1, while plantation forests (rotation $\leq$ 15 years) had the highest CWV-PC2, CWV-PC3, CWV-PC4, and CWV-PC5 levels (Figure 2).

Table 1. The loading matrix of principal component analysis (PCA) for CWM and CWV, respectively.

Trait	CWM-PC1	CWM-PC2	CWM-PC3	CWV-PC1	CWV-PC2	CWV-PC3	CWV-PC4	CWV-PC5
Leaf area	0.241	0.334	0.028	**0.312**	−0.091	−0.006	−0.605	0.049
Stem-specific density	0.306	−0.089	−0.081	0.149	−0.012	0.138	−0.009	−0.154
Specific leaf area	−0.162	**0.448**	0.033	**0.346**	−0.164	−0.322	0.162	0.105
Leaf carbon concentration	0.046	0.087	−0.056	0.130	−0.006	0.080	0.122	0.448
Leaf nitrogen concentration	−0.055	**0.433**	0.105	0.186	−0.187	0.173	0.174	0.275
Leaf phosphorus concentration	−0.230	0.257	**0.384**	0.156	−0.168	**0.463**	0.136	0.272
Mean plant height	**0.340**	−0.074	0.192	**0.301**	0.070	−0.315	0.102	−0.075
Seed mass	**0.356**	0.083	0.218	0.194	**0.518**	0.034	0.068	0.015
Seed length	**0.322**	0.064	0.348	0.189	**0.518**	0.141	0.028	0.005
Leaf dry matter content	0.207	−0.351	−0.005	0.189	−0.176	0.119	0.117	**−0.532**
Leaf N per area unit	0.199	−0.301	0.018	**0.313**	−0.156	−0.282	0.203	0.087
Leaf N:P ratio	0.279	0.097	−0.361	0.181	−0.133	**0.447**	0.087	0.092
leaf δ15N	0.101	0.043	−0.304	0.149	0.009	0.293	0.067	0.003
Seed number per reproductive unit	−0.165	−0.153	0.209	0.273	−0.035	−0.059	0.136	−0.107
Fresh leaf mass	0.280	0.242	−0.004	0.287	−0.097	0.060	**−0.645**	0.015
Stem conduit density	−0.195	−0.242	0.253	0.270	−0.071	−0.284	0.081	0.145
Dispersal unit length	0.296	0.035	**0.416**	0.250	0.493	0.079	0.011	−0.066
Wood vessel element length	0.128	0.189	−0.347	0.199	−0.168	0.181	0.140	**−0.521**

The bold values indicate the strongest relationships of principal components (PCs) with CWM and CWV, with a significance of $p < 0.05$.

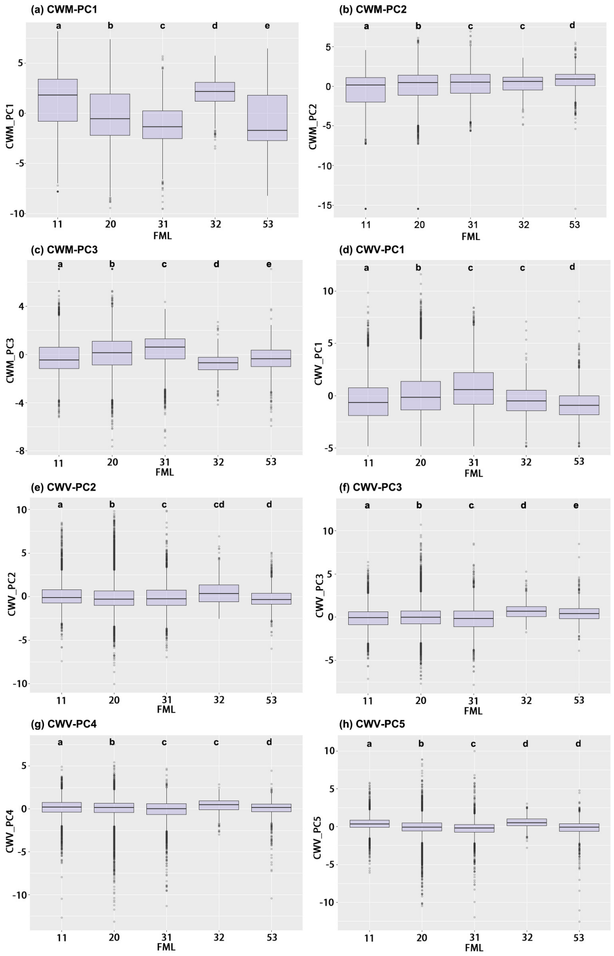

Figure 2. Changes in the CWM-PCs and CWV-PCs across five forest management types based on post hoc Tukey tests. The codes of forest management types were followed from the study of Lesiv et al. (2022) [13]: 11, intact forests; 20, managed forests with natural regeneration; 31, planted forests; 32, plantation forests (with up to a 15-year rotation); and 53, agroforestry. Different letters represent significant differences in Tukey's post hoc testing. Each point represents one transect (five per forest management type); boxplots represent the median (centre line), interquartile range (boxes), and full range (whiskers).

Moreover, we found that the conversion from natural to plantation forests resulted in different levels of RR values for CWM-PCs and CWV-PCs depending on the changes in ecozone types (Figure 3). Overall, plantation forests were positively related to the CWM and CWV across different forest ecozones based on the RR assessment. However, the lowest values were observed in tropical and subtropical coniferous forests (Figure 3). However, the degrees of responses of the CWM and CWV to plantation were different due to the ecozone type changes (Figure 3). Significant differences between natural and plantation forests were observed for all the CWM-PCs and CWV-PCs in temperate broadleaf and mixed forests and temperate coniferous forests (Figure 3). Plantation forests exhibited a positive effect on CWM-PC3 and negative effects on CWV-PC4 in boreal forests/taiga (Figure 3). Plantation forests only negatively affected CWM-PC3 and CWV-PC4 in tropical and subtropical coniferous forests and CWV-PC2 in temperate broadleaf and mixed forests. Plantation forests had the largest positive effects on CWM-PC3 in broadleaf forests, as well as on CWV-PC4 in temperate coniferous forests, and CWV-PC5 in tropical and subtropical moist broadleaf forests (Figure 3).

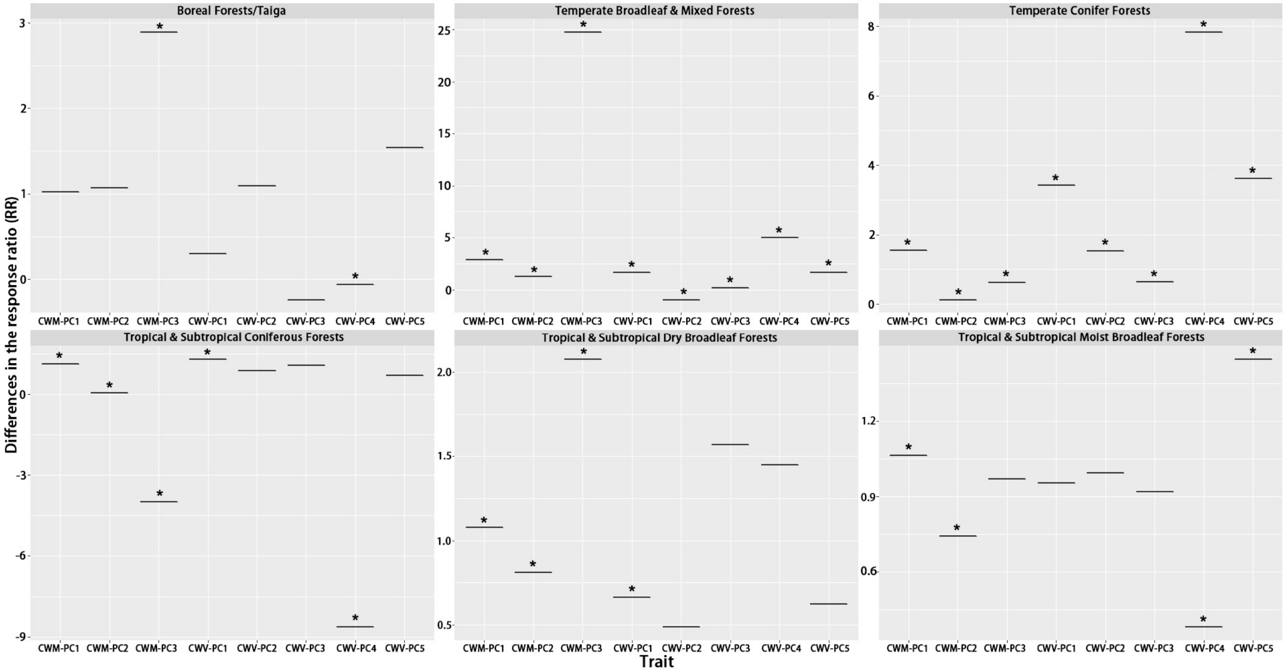

Figure 3. Differences in the response ratio (RR) of CWM-PCs and CWV-PCs in plantation forests (i.e., planted forests and agroforestry) compared to natural forests (i.e., intact forests and managed forests with natural regeneration). * Indicates significant differences in RR results between plantation forests (i.e., planted forests and agroforestry) compared to natural forests (i.e., intact forests and managed forests with natural regeneration) based on ANOVA tests.

4. Discussion

4.1. Linking Forest Management to CWM and CWV

Different forest management types lead to variation in environmental conditions, such as microclimate, soil type, humus content, and water content, thereby affecting the CWM and CWV. In addition, different forest types have variations in species composition, which affects the CWM and CWV of the entire plant community. This study contributes to understanding how forest management can influence the FCPC using CWM and CWV, which are closely associated with ecosystem functions and services [6–8,27]. We found that plantation forests (rotation $\leq$ 15 years), planted forests (rotation > 15 years), and agroforestry positively affected the CWM and CWV to an even greater extent than intact forests and natural forests. The PCs that we extracted can explain more than half of the variance, so management should be undertaken in order to increase the CWM and

CWV values. Hua et al. (2022) demonstrated the changing trends of ecosystem functions and services in natural and plantation forests worldwide [12]. Our results suggest that forest management is closely linked to plant functional trait variations, in agreement with Hua et al. (2022) [12]. Our results provide a reference for forest ecological restoration from the perspective of plant functional traits [4]. Taken together, these results demonstrate the utility of applying plant functional traits to guide forest management based on ecosystem functions and services.

Interestingly, we found that the relationship between forest management and the CWM and CWV is significantly affected by the forest management types. Specifically, forest management types are defined by the duration of forest restoration as renaturation without any human intervention as a natural succession forest, or ecological restoration with human-assisted turn back to a bunch of forest species that disappeared meanwhile from a specific location [12,13]. Different trait values become important for species' succession at different points along succession gradients [29,30]. We found that plantation forests (rotation $\leq$ 15 years) had a large contribution to the mean plant height, seed mass, and seed length based on the CWM and CWV, indicating that early plantation can regulate species dispersal limitations in forests [4,31]. The dispersal limitations play an essential role in ecological changes in the early successional stages of forests with a rotation $\leq$ 15 years [32,33]. Habitat fragmentation may widely exist in the early stages of plantation forests [34,35]. Short-lived plants with non-dormant seeds and long-distance dispersal are most vulnerable to habitat fragmentation [36,37]. There is a positive association between seed mass and plant height [37]. Hence, we can target an increased plant height and seed size to further promote ecosystem functions and services under forest restoration.

Our results showed that in planted forests (rotation > 15 years), there are strong effects on leaf traits (i.e., CWM-PC3 and CWV-PC1; leaf phosphorus concentration, leaf area, and specific leaf area). A longer-timeframe successional stage may drive the changes in plant leaf traits [38,39]. Species with a lower specific leaf area are considered worse light competitors but may be better competitors in undersoil nutrient limitations of old forests [40–42]. Short stature and low-specific-leaf-area weedy species may be important drivers of trait composition during prairie restoration either through their establishment or their influence on the establishment of other species through competition [41,43,44]. Old, planted forests can positively impact and increase leaf phosphorus concentration by enhancing enzymatic activities. High enzyme activities can promote the wood-forming tissues in trees and the recovery of forest ecosystems [45,46]. Hence, planted forests (rotation > 15 years) can lead to changes in ecosystem functions and services, affecting the ecological restoration processes, and are integral for a successful restoration strategy.

Forest restoration is being scaled-up globally to deliver critical ecosystem functions, services, and biodiversity benefits [12,47–49]. Hua et al. (2022) showed that carbon storage and biodiversity benefits are all better delivered by intact forests, and wood production is significantly higher in plantation forests [12]. Our results showed that effective plantation and agroforestry management could contribute to ecosystem services (e.g., wood production) due to the dispersal limitation and wood development using the CWM and CWV as ecological indicators. Our study provided evidence that forest management could support ecosystem functions, particularly in plantations.

4.2. Ecozone Effects

Based on our results, the conversion from natural to plantation forests could lead to different levels of CWM-PCs and CWV-PCs depending on the different ecozone types, indicating that the effects of forest restoration on plant functional traits depend on the ecozone properties and changes. Overall, plantation forests positively affected the CWM and CWV across different forest ecozones. Plantation forests negatively affected CWM-PC3 and CWV-PC4 in tropical and subtropical coniferous forests and CWV-PC2 in temperate broadleaf and mixed forests. These results suggest that forest management types (i.e., plantation) can regulate the variability of ecosystem functions and services across different ecozone types [2–5].

Moreover, the influence levels of plantation on the CWM and CWV are different across the variation in forest ecozones. The FCPC can be used as an important indicator for monitoring forest restoration. We found significant differences between natural and plantation forests across all the CWM-PCs and CWV-PCs in temperate broadleaf and mixed forests and temperate coniferous forests. The CWM and CWV are shaped by environmental factors [6,50]. Understory vegetation can affect forest tree regeneration and soil temperature and soil processes (e.g., organic matter decomposition and nitrogen mineralization) [50]. Soil conditions and understory vegetation are altered along the restoration process after plantation [51–54]. Furthermore, the CVM and CWV of seed and leaf traits vary across different forest types due to alterations in understory plant communities and soil physical and chemical properties [51,52,55]. The FCPC can be used as a biological indicator for forest management practices to improve the forest ecosystems' sustainability.

Finally, we found that forest plantation had the largest positive effects on CWM-PC3 in boreal forests/taiga, temperate broadleaf and mixed forests, and tropical and subtropical dry broadleaf forests, as well as on CWV-PC4 in temperate coniferous forests, and CWV-PC5 in tropical and subtropical moist broadleaf forests. These results indicated that the leaf phosphorus concentration (i.e., CWV-PC3) and leaf dry matter content (i.e., CWV-PC5) could be effectively regulated through forest management across ecozones. The leaf phosphorus concentration could be implemented as an effective ecological indicator of forest restoration for boreal forests/taiga, temperate broadleaf and mixed forests, tropical and subtropical dry broadleaf forests, and temperate coniferous forests. These ecozones have relatively dry climate conditions that affect leaf phosphorus concentration [20,21]. Phosphorus-induced enzyme activities should be monitored to manage dry ecosystems under forest plantations [56]. The leaf dry matter content is directly related to litter decomposition, a critical step for carbon and nutrient turnover, determining the carbon balance in tropical and subtropical moist broadleaf forests [57–60]. Hence, the plantation is a crucial factor in understanding how sunlight controls carbon and nutrient dynamics in various ecosystems and is essential to accurately assess how biogeochemical cycles might respond to global changes (e.g., land use change).

5. Conclusions

We conclude that forest management types are able to reflect ecosystem functions and services based on the FCPC (i.e., CWM and CWV). We could manage ecosystems by observing the FCPC. Forest ecosystems should be managed to increase CWM and CWV levels, which could contribute to ecosystem functions and services. Although the relationship between the plant communities' functional composition and ecosystem functions may not be linear, the increase in the CWM and CWV can positively impact the ecosystem functions and services during forest restoration processes, depending on the ecozone types. It is therefore possible that the crucial plant functional traits can be predicted for ecosystem maintenance and biodiversity conservation. Adding to the study of Hua et al. (2021) that quantified ecosystem functions and services across natural and plantation forests, our results have further contributed to the evidence-based mechanism study for ecosystem functions and services [12]. Future studies should explore the deep understanding of the mechanisms that link the FCPC to ecosystem functions and services under different forest management practices.

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