Species Diversity of Deadwood in Chinese Fir Plantations Differs between Mixed Planting and Thinning Treatments

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Abstract: The occurrence of deadwood is inevitable during the process of plantation conversion, but the influences of conversion and the potential environmental effect on deadwood species diversity remain unclear. We established two fixed plots in Chinese fir thinned forest (TF) and Chinese fir and Michelia macclurei Dandy mixed forest (MF) (100 × 80 and 120 × 60 m², respectively). We classified the deadwood into groups based on origin and by status, and analyzed deadwood species diversity using four common diversity indices. We also investigated the contribution of topographic factors to tree mortality using redundancy analysis. The species composition of deadwood differed markedly between the MF and TF. The species diversity and variety of deadwood status were greater for the TF than MF, although abundance was lower. Topography was poorly correlated with deadwood in the MF, while in the TF, altitude was strongly correlated with deadwood from Chinese fir, shade-intolerant late-coming populations, and fallen wood. Slope was negatively correlated with late-coming populations and fallen wood, but deadwood correlations with convexity were weak. These results indicate that cultivation methods strongly alter the species composition, status, abundance and diversity of deadwood in plantations. Topographic factors and targeted cultivation practices promote the formation of deadwood.

Keywords: deadwood; mixing; plantation; species diversity; thinning; topography

1. Introduction

Planted forests (hereinafter referred to as plantations) account for about 7% of the world’s total forest area [1]. They are often managed intensively, through single-species cultivation and rotation harvest (the circulation of a period from afforestation to harvest) [2], to maximize short-term wood supplies and income and alleviate tension between the supply of and demand for wood resources [3,4]. However, many ecological problems have arisen in monoculture plantations, such as the simple stand structure, low species diversity, annual decline of productivity and site quality, and outbreaks of diseases and insect pests, which seriously threaten the sustainable development of forests, and the wider ecological environment [5–7]. To ensure that plantations are better adapted to site conditions, able to resist various disturbances [8,9], and amenable to sustainable management at the stand, local, regional, and even global levels, multiple tree species can be planted directly; alternatively, existing monoculture plantations can be converted into mixed forest [7,10].

Tree death is inevitable in the process of cultivation and conversion of MF. In the early stage of cultivation, site selection, nursery practices, planting design, fertilization,
pest control, and stand tending are important to promote tree growth and reduce size differences and mortality [11,12]. To reduce stand density and accelerate growth in the stem exclusion phase, thinning should be carried out for long-lived species [13]. During thinning operations, unintentional human and mechanical damage can lead to the death of understory and retained trees [11,14]. Factors such as competition between neighboring trees, negative density dependence, senescence, pests and diseases, and natural disasters, such as lightning strikes, typhoons, slope collapse and floods, lead to the formation of deadwood in mature and old-growth stands [7,15,16]. Abiotic factors including topography and related factors (e.g., climate, temperature, moisture), which are easily overlooked in plantation cultivation, might also contribute to tree death [5,17,18]. Deadwood in plantation operations is often ignored [11] or removed [15].

Chinese fir (Cunninghamia lanceolata (Lamb.) Hook.) is a fast-growing, high-quality timber species for plantation, with a very long (800–1000 years) cultivation history in China [10,19–22]. Beginning in the 1950s, a large number of Chinese fir plantations have been cultivated in public and state-owned forestland in southern China (e.g., in Guangxi, Guizhou, Jiangxi, Hunan, Zhejiang and Fujian Provinces). These plantations are widely distributed in valleys, depressions, ridges, and mountaintops, and even on steep slopes [23]. With the rapid expansion of plantation areas, increase in continuous cultivation, and shortening of timber rotations [24,25], the drawbacks of Chinese fir mono-specific plantations have gradually emerged [4,23]. Many stands have suffered from site decline, and some of them have become small-sized, old forests in which trees grow slowly and have low economic value [2]. Such stands are candidates for conversion. Understory planting, thinning [10,26], delayed harvesting after thinning [22,27], and hillsides facilitate afforestation [4], and have been used to promote the “near-natural conversion” of Chinese fir plantations. Typically, managers have had a short-term focus on interplanted living organisms and converted forests, including the growth rates and diversity of herbs, shrubs, and trees. In mountainous areas, it is not yet clear how these cultivation practices affect the formation of deadwood.

In the early 1990s, near-natural conversion experiments were conducted in Chinese fir plantations in a mountainous state-owned forest farm in southern China. In line with previous studies on the conversion of Chinese fir plantations [19,20], it has been found that both thinning and interplanting promoted complex stand structures and species diversity [2,7]. Soil organic carbon, total nitrogen and total phosphorus were higher in the MF than in the thinned forest (TF) [28], and the MF were more conducive to the formation of stable aggregates in surface soil [29]. In this study, the effects of thinning and species mixing on the diversity of deadwood in these Chinese fir plantations are further examined. The following hypotheses are tested: thinning creates gaps and introduces additional tree species, and TF will therefore have higher diversity of deadwood than the MF (hypothesis 1); in the absence of obvious natural disturbance, thinning may cause the death of other trees, such that there will be more trees of deadwood status in the TF than in the MF (hypothesis 2); commonly planted species (PS) are large, while late-coming populations (LCPs) are small, and topography has a greater effect on LCPs than PS (hypothesis 3).

2. Materials and Methods

2.1. Study Area

Our study site was located in the Experimental Center of Tropical Forestry of the Chinese Academy of Forestry, Pinxiang, Guangxi Zhuang Autonomy Region, China (21°57’01”–22°16’00” N, 106°41’06”–106°59’06” E). The experimental center was established in 1927, the management area is 18,900 ha, and the forest stock amounts to 1,450,000 m$^3$. The experimental center undertakes scientific experiments concerning southern subtropical forestry; these involve the collection, conservation and utilization of forest germplasm resources, cultivation of precious tree species, investigations of ecological services and functions of plantations, restoration of vegetation in rocky areas and management of forest
resources. The region lies in the south subtropical monsoon climate zone. The annual rainfall is about 1200–1500 mm during the April to September rainy season, and the annual precipitation is about 1300–1700 mm. The relative humidity is 80–84%. The mean annual temperature in the region ranges from 19.5 to 21.5 °C, with the lowest temperature of −1.5 °C occurring in January, and the highest temperature of 40.3 °C occurring in July. The annual accumulated temperature is 7518.4 °C. The area is usually frost-free throughout the year.

The landforms in this region include hills, platforms, mountains, karst formations, and valley terraces. The highest peak in the region is Daqing Mountain, which is 1045.9 m above sea level. The soils are red soils and latosols formed by the weathering of granite and intermediate-acid volcanic rocks, and have an acid pH of 4.8–5.5. Soil layers are generally deep and loose, with a mean thickness of 50–100 cm [29]. The original vegetation of the experimental center was completely destroyed and replaced by decertified commercial forests [2,4,7,11]. Many tree species, including Chinese fir, *Pinus massoniana* Lamb., *Eucalyptus*, *Castanopsis hystrix* Miq., *Michelia macclurei* Dandy, *Manglietia glauca* Blume, and *Betula alnoides* Buch.-Ham. ex D. Don, have been widely planted. Chinese Fir has been cultivated for more than half a century in this area.

### 2.2. Test Design and Plot Establishment

In the spring of 1991, we constructed a mixed forest (MF) of Chinese fir and *M. macclurei* in the third compartment (106°42′16″ E, 22°18′09″ N) of the Daqing Mountain sub-forestry farm. Both Chinese fir and *M. macclurei* were seedlings, planted at a ratio of 6:1. After random mixing, they were planted regularly. The initial planting density was 2000 plants ha⁻¹, and the seedling survival rate was about 87% after 2 years. During the first 3 years after planting, fertilization was carried out, among other tending activities. At the same time, we planted a Chinese fir monoculture stand in the sixth compartment (106°42′48″ E, 22°17′44″ N); the planting and cultivation practices were the same as those used in the MF. After 2 years, the survival rate was also 87%. In 2008, we randomly cut 631 Chinese fir (basal area, 15.13 m²/ha) with diameter at breast height (DBH) ≥ 9 cm [2,7,11]. Since then, the stand has been free from human disturbance, and has developed into a mixed forest with many tree species. Many pieces of deadwood were found in the forest.

In 2018, we established two standard plots: one with an area of 120 m × 60 m in the MF, and another 100 m × 80 m plot in the TF (Figure 1). First, we used a global positioning system to select the sample area and determine its longitude, latitude, and altitude. The average elevation and slope were 755 m and 27° in the MF, and 710 m and 32° in the TF, respectively (Figure 1). Second, we used a total station (NTS-372R10; South Surveying and Mapping Company, Guangzhou, China) to accurately locate the borders of the plots (closure difference < 1/400), which were then divided into 20 m × 20 m quadrats. We fixed polyvinyl chloride pipes at each cross point of the smaller quadrats, as permanent markers, and connected each small quadrat using red rope. Third, we obtained the coordinates (x, y, z) of all deadwood pieces (including snags, fallen wood and broken wood) and trees in the quadrat on an individual basis. Finally, we tallied, counted, marked, and recorded all objects with DBH ≥ 1 cm [11]. We measured 1909 live trees (2651 individuals/ha; 35.81 m²/ha), 304 snags (standing deadwood), and 254 pieces of fallen wood in the MF, and 3,084 live trees (3855 individuals/ha; 40.19 m²/ha), 111 snags, 66 pieces of fallen wood, 41 pieces of broken wood, and 639 stumps in the TF (see Table S1). The mortality rate of Chinese fir was 44.97% in the MF and 19.85% in the TF [2,11].
Figure 1. The study plots, located on the mid–slope of Daqing Mountain. Green squares indicate the location and size of plots, and Arabic numerals indicate compartment number. Subfigures (a,b) represent the terrain of quadrats in the MF and TF, respectively.

2.3. Data Analysis

We classified deadwood into two categories according to origin and status. The origin types include PS and LCPs. The PS in the TF was Chinese fir, and those in the MF were Chinese fir and *M. macclurei*. The LCPs consisted of populations of many other species. Deadwood statuses included snags, fallen wood and broken wood. We analyzed deadwood species diversity and its relationship with topography.

2.3.1. Extraction of Terrain Factors

We imported the coordinate data (x, y, z) into ARCGIS 10.2 ([https://www.esri.com/en-us/arcgis/](https://www.esri.com/en-us/arcgis/) (accessed on 25 August 2021)) to create a digital elevation model (DEM) of the quadrats, and calculated the elevation (m), convexity, slope (in degrees), and aspect for each of them. Elevation was recorded as the average elevation of the four vertex angles of each quadrat, and convexity as the elevation at the center of each quadrat minus its average elevation. A positive convexity value indicated that the quadrat center was higher than the surrounding area; a negative value indicated that the center was lower than its surroundings, and zero indicated that the convexity was small. Slope was recorded as the mean angle of the four planes formed by any three vertices in the quadrat. Aspect was represented by the mean value of the angle between true north and the orientation of the four planes comprising the three vertices.

2.3.2. Species Diversity

We analyzed the diversity of deadwood using four common indexes of species diversity: the Margalef index ($D_M$), Shannon–Wiener index ($H'$), Simpson index ($D$), and Pielou’s evenness index ($J_{SW}$) (Table 1). The data were visualized using a boxplot, and the significance of differences between stands was tested using the Kruskal–Wallis test. Data analyses were performed in R ([https://www.r-project.org/](https://www.r-project.org/) (accessed on 31 December 2021)).
2023) using the Vegan package [30]. We compared the difference of deadwood species composition between the MF and TF using principle coordinate analysis (PCoA), and the significance was tested using ADONIS analysis. We investigated the effects of topographic factors on species and deadwood diversity, according to deadwood origin and status, using a redundancy analysis (RDA). Terrain factors were analyzed using a permutation test (repeated 999 times) performed in Canoco 5.0 software [31].

Table 1. Indices of species diversity used in this study.

<table>
<thead>
<tr>
<th>Indices</th>
<th>Formulas</th>
<th>Explanation</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Margalef index ((D_M))</td>
<td>(D_M = \frac{SR - 1}{\ln N})</td>
<td>(SR =) species richness, (N = ) total number of individuals</td>
<td>[32]</td>
</tr>
<tr>
<td>Simpson index ((D))</td>
<td>(D = 1 - \sum_{i=1}^{SR} \left( \frac{P_i^2}{P_i} \right))</td>
<td>(P_i = ) relative abundance of the (i)th species; (SR =) species richness</td>
<td>[32]</td>
</tr>
<tr>
<td>Shannon–Wiener index ((H'))</td>
<td>(H' = - \sum_{i=1}^{SR} \left( P_i \cdot \ln P_i \right))</td>
<td>(SR =) species richness; (H' =) Shannon–Wiener index</td>
<td>[32]</td>
</tr>
<tr>
<td>Pielou evenness index ((JSW))</td>
<td>(JSW = \frac{H'}{\ln SR})</td>
<td>(SR =) species richness, number of species</td>
<td>[33]</td>
</tr>
</tbody>
</table>

3. Results

3.1. Species Composition of Deadwood

The species composition and origins (LCPs, PS) of the MF and TF were remarkably different (Figures 2a–c and 3a–c). In the MF, PS contributed 97.1% of the deadwood, and included 536 Chinese fir and 6 \textit{M. macclurei}, while LCPs accounted for only 2.9%, and included 10 recognizable and 6 unrecognizable pieces (Table 2). The recognizable LCPs belonged to 5 species from 5 different genera in 5 families. In the TF, there were 162 PS and 56 LCPs, and the LCPs included 14 species from 10 families (Table 2). In addition to Chinese fir, MF and TF have 3 common LCPs: \textit{Litsea variabilis} Hemsl., \textit{Evodia lepta} (Spreng.) Merr., and \textit{Saurania tristyla} DC (Figure 2, Table 2).

![Figure 2](image-url)

**Figure 2.** Venn diagram showing the difference in deadwood composition within different origins (a–c) and status (d–f) between the MF and TF. The numbers in circles indicate species richness. The red circle represents MF, while blue represents TF. Overlapping areas indicate that the MF and TF share the same species.
red circle represents MF, while blue represents TF. Overlapping areas indicate that the MF and TF share the same species.

Figure 3. Results of PCoA analysis of deadwood differing in origin (a–c) and status (d–f). p-values indicate the result of ADONIS analysis. p > 0.05, not significant; *** (p < 0.001), extremely significant.

Table 2. The quantitative characteristics of deadwood within different origins.

<table>
<thead>
<tr>
<th>Stands</th>
<th>Origin</th>
<th>Family</th>
<th>Species</th>
<th>Abbreviation</th>
<th>N</th>
<th>DBH (Mean ± SD) (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MF</td>
<td>LCPs</td>
<td>Actinidiaceae</td>
<td>Saurauia tristyla DC.</td>
<td>ST</td>
<td>1</td>
<td>4.20</td>
</tr>
<tr>
<td>MF</td>
<td>LCPs</td>
<td>Alangiaceae</td>
<td>Alangium faberi Oliv</td>
<td>AFo</td>
<td>1</td>
<td>3.80</td>
</tr>
<tr>
<td>MF</td>
<td>LCPs</td>
<td>Lauraceae</td>
<td>Litsea variabilis Hemsl.</td>
<td>LV</td>
<td>2</td>
<td>5.15 ± 0.35</td>
</tr>
<tr>
<td>MF</td>
<td>LCPs</td>
<td>Magnoliaceae</td>
<td>Michelia macclurei Dandy</td>
<td>MMd</td>
<td>3</td>
<td>8.87 ± 3.95</td>
</tr>
<tr>
<td>MF</td>
<td>LCPs</td>
<td>unknown</td>
<td>unknown</td>
<td>UNK</td>
<td>6</td>
<td>7.35 ± 6.37</td>
</tr>
<tr>
<td>MF</td>
<td>PS</td>
<td>Magnoliaceae</td>
<td>Michelia macclurei Dandy</td>
<td>MMd</td>
<td>6</td>
<td>19.02 ± 2.97</td>
</tr>
<tr>
<td>MF</td>
<td>PS</td>
<td>Cupressaceae</td>
<td>C. lanceolata</td>
<td>CL</td>
<td>536</td>
<td>10.96 ± 3.75</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Actinidiaceae</td>
<td>Saurauia tristyla DC.</td>
<td>ST</td>
<td>5</td>
<td>4.48 ± 2.19</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Ebenaceae</td>
<td>Diospyros morrisiana Hance</td>
<td>DM</td>
<td>1</td>
<td>8.00</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Euphorbiaceae</td>
<td>Mallotus philippensis (Lam.) Muell. Arg.</td>
<td>MP</td>
<td>1</td>
<td>6.80</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Fagaceae</td>
<td>Castanopsis hystrix Miq.</td>
<td>CH</td>
<td>2</td>
<td>2.65 ± 0.15</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Hamamelidaceae</td>
<td>Mytilaria lasiossis Lec.</td>
<td>MLI</td>
<td>2</td>
<td>13.50 ± 1.50</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Lauraceae</td>
<td>Litsea variabilis Hemsl.</td>
<td>LV</td>
<td>1</td>
<td>3.80</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>Magnoliaceae</td>
<td>Michelia chinensis (Champ. ex Benth.) Hemsl.</td>
<td>MC</td>
<td>1</td>
<td>6.20</td>
</tr>
<tr>
<td>TF</td>
<td>LCPs</td>
<td>unknown</td>
<td>unknown</td>
<td>UNK</td>
<td>25</td>
<td>6.64 ± 3.83</td>
</tr>
<tr>
<td>TF</td>
<td>PS</td>
<td>Cupressaceae</td>
<td>C. lanceolata</td>
<td>CL</td>
<td>162</td>
<td>13.71 ± 5.92</td>
</tr>
</tbody>
</table>

The species composition of deadwood varied with deadwood status (p < 0.01) (Figures 2d–f and 3d–f). Snags and fallen deadwood accounted for 54.5% and 45.5% of the deadwood in the MF, respectively. MF had 254 pieces of fallen wood, all of which came from PS, including 252 Chinese fir and 2 M. macclurei. There were also 304 pieces of snags,
they belonged to 7 species from 6 families, including 288 PS and 16 LCPs (Table 3). In the TF, snags and fallen deadwood accounted for 50.9% and 30.3%, and broken wood for 18.8%. There were 66 pieces of fallen wood, including 51 Chinese fir, 11 *E. lepta*, 2 *Mytilaria laosensis* Lec., 1 *Wendlandia warriophila* Hance, and 1 *S. tristyla*. The TF also had 111 snags, including 71 Chinese fir, and 40 LCPs that belonged to 14 families. In the TF, there were pieces of 40 broken wood from Chinese fir, and 1 piece from *W. uvarifolia* (Table 3).

Table 3. The quantitative characteristics of deadwood within different statuses.

<table>
<thead>
<tr>
<th>Stands</th>
<th>Statuses</th>
<th>N</th>
<th>SR *</th>
<th>DBH (Min-Mean-Max) (cm)</th>
<th>Height/Length (Min-Mean-Max) (m)</th>
<th>Basal Area (cm²)</th>
<th>Volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MF</td>
<td>Fallen wood</td>
<td>254</td>
<td>2</td>
<td>1.5-9.5-20.0</td>
<td>1.3-5.8-14.0</td>
<td>71.2</td>
<td>14.7</td>
</tr>
<tr>
<td></td>
<td>Snags</td>
<td>304</td>
<td>7</td>
<td>2.5-12.1-25.0</td>
<td>1.3-4.8-13.0</td>
<td>114.9</td>
<td>34.7</td>
</tr>
<tr>
<td>MF</td>
<td>Fallen wood</td>
<td>66</td>
<td>5</td>
<td>3.0-10.6-12.0</td>
<td>1.0-5.3-16.0</td>
<td>87.9</td>
<td>5.7</td>
</tr>
<tr>
<td>TF</td>
<td>Snags</td>
<td>111</td>
<td>14</td>
<td>1.2-9.8-26.0</td>
<td>0.5-9.4-19.2</td>
<td>75.1</td>
<td>11.2</td>
</tr>
<tr>
<td>TF</td>
<td>Broken wood</td>
<td>41</td>
<td>2</td>
<td>4.5-17.6-21.0</td>
<td>1.3-5.1-14.0</td>
<td>242.7</td>
<td>11.9</td>
</tr>
</tbody>
</table>

* SR indicates the species richness.

3.2. Species Diversity of Deadwood

The values of species diversity indices (*SR, D_M, D, H’, JSW*) in the TF differed between deadwood and LCPs (deadwood: 15, 2.600, 0.432, 1.063; LCPs: 14, 3.230, 0.756, 1.918, respectively), and were significantly higher than those in the MF (deadwood: 7, 0.949, 0.077, 0.222; LCPs: 6, 1.846, 0.755, 1.587, respectively) (*p* < 0.05) (Figures 4a–d and 5f–i). The *JSW* of deadwood was significantly higher in the TF than MF (Figure 4e), while for LCPs, it was lower in the TF than MF (Figure 4j). All the values of diversity indices of PS in the TF were significantly lower than in the MF (Figure 4k–n).

![Figure 4](image-url). Boxplots of *SR, D_M, H’, D, H’, JSW* according to the origins of deadwood and stands, subfigures (a–e) indicate the deadwood, (f–j) indicate the LCPs, (k–o) indicate the PS. Black dots indicate species diversity and evenness indices in the MF and TF. *p*-values are for the results of the Kruskal–Wallis test, *p* > 0.05, not significant; * (0.01 < *p* < 0.05), significant; ** (*p* < 0.01), highly significant.
3.3. Correlations between Topographic Factors and Deadwood Distribution

In the MF, the proportion of variance explained by the first two axes of the RDAs for deadwood, LCPs, and PS was 27.4%, 14.21%, and 44.89%, respectively (Figure 6a–c), and was 40.30% and 20.24% for fallen wood and snags, respectively (Figure 7a,b). In the TF, the sums of the first two axes for deadwood, LCPs, and PS were 37.14%, 36.96%, and 100.00%, respectively (Figure 6d–f). The first two RDA axes for fallen wood, snags, and broken wood amounted to 34.06%, 32.36%, and 40.63%, respectively (Figure 7c–e). There was no significant correlation between topographic factors and deadwood in the MF ($p > 0.05$) (Figures 6a–c and 7a,b). In the TF, elevation was positively correlated with PS (i.e., Chinese fir) and some LCPs (Evodia lepta, M. laosensis and Ficus hirta Vahl), while slope was negatively correlated with these LCPs (Figure 6e). Elevation was positively correlated with fallen wood (Evodia lepta, M. laosensis and Chinese fir) (Figure 7c); however, broken wood was not significantly correlated with topographic factors (Figure 7e). In general, convexity and aspect had little correlation with the distribution of deadwood (Figures 6 and 7).
Figure 5. Boxplots of SR, DM, H', D, and JSW, based on the status of deadwood and stands, subfigures (a–c) indicate the species diversity and evenness indices in the MF and TF. The p–values are derived from the permutation test for topographic factors, p > 0.05, not significant; * (0.01 < p < 0.05), significant; ** (p < 0.01), extremely significant. See Table 2 for the key for the abbreviations.

Figure 6. RDA ordination biplots of deadwood with different origins in the MF (a–c) and TF (d–f). The red arrows indicate species, and black arrows indicate topographic factors. The p–values are derived from the permutation test for topographic factors, p > 0.05, not significant; * (0.01 < p < 0.05), significant; ** (p < 0.01), extremely significant. See Table 2 for the key for the abbreviations.

Figure 7. RDA ordination biplots according to deadwood status in the MF (a,b) and TF (c–e). The red arrows indicate species, and black arrows indicate topography factors. The p–values are derived from the permutation test for topographic factors, p > 0.05, not significant; * (0.01 < p < 0.05), significant. See Table 2 for the key for the abbreviations.
3.4. Correlations between Topographic Factors and Deadwood Species Diversity

The first two axes summed to 18.64%, 100%, 100%, and 35.85% for the species diversity of deadwood, LCPs, PS, and snags in the MF, respectively (Figure 8a–d). The equivalent axis sums of TF were 50.77%, 60.12%, 67.46%, and 55.8% for deadwood, LCPs, fallen wood, and snags, respectively (Figure 8e–h). Topographic factors were not significantly correlated with deadwood species diversity in the MF (Figure 8a–d). In the TF, elevation was positively correlated with SR, DM, D, and $H'$ for deadwood and snags, as well as with SR and $H'$ for LCPs and fallen wood (Figure 8e–h). Significant negative correlations were observed between the slope and SR of deadwood and snags, and between the slope and SR and $H'$ of LCPs and fallen wood ($p < 0.05$). There were no significant correlations between topographic factors and $J_{SW}$ (Figure 8e–h). Convexity and aspect had little impact on the species diversity of deadwood in either stand ($p > 0.05$) (Figure 8).

Figure 8. RDA ordination of deadwood species diversity and evenness ($SR, DM, H', D, J_{SW}$) in the MF (a–d) and TF (e–h). The red arrows indicate indices of species diversity, and the black arrows indicate topography factors. The $p$–values are the results of permutation tests of topographic factors, $p > 0.05$, not significant; * ($0.01 < p < 0.05$), significant; ** ($p < 0.01$), highly significant, *** ($p < 0.001$), extremely significant.
4. Discussion

Deadwood plays a key role in maintaining the stability and balance of forest ecosystems. It provides a habitat and food resources for wildlife, promotes the natural regeneration and tree growth, and stores forest carbon [15,16,34–36]. The extraction of large-diameter trees from cultivated plantations reduces both the potential sources and input pathways for deadwood formation, and thus significantly reduces the quantity and quality of deadwood [34,36]. However, more attention has been paid to improving the biodiversity of plantations, including their deadwood [37], with recent changes to plantation management strategies and forest policies, and with greater understanding of forest ecosystem function [38]. Thinning and species mixing have become the main approaches to enhance biodiversity in plantation forests [10,39].

Substantial quantities of deadwood were observed in the MF and TF. The amount of deadwood in the MF was much higher than in the TF, indicating that light thinning reduces intraspecific competition and significantly reduces mortality in PS [40]. Chinese fir dominated the deadwood in both stands, suggesting that intensely intraspecific competition occurred in the MF, which was planted with two cultivated species in a 6:1 ratio. Chinese fir and *M. macclurei* differ in morphology, growth rhythm [19], and photosynthetic dynamics [7]. Mixed stands of these species significantly increased productivity and improved the microclimate of the tree canopy, stand interior, and soil (e.g., soil physical and chemical properties, nutrient concentrations, and microorganism communities) [19,20] at the early stage of planting. However, *M. macclurei* markedly suppressed Chinese fir after the middle stage, which may lead to mortality [7,11]. Stem analysis revealed a similar competitive dynamic in an MF of Chinese fir and *Tsoongiodendron odoratum* [41]. Adjusting the planting ratio and competitive relationship among sympatric populations could promote the formation of dead trees.

In this study, the species richness and diversity indices of deadwood in the TF were much higher than those in the MF, consistent with our hypothesis 1. This suggested that thinning promoted the regeneration and growth of multiple species [13,42–44], which eventually became sources of deadwood. Several studies of Chinese fir plantations showed that the number of herbaceous species and shade-intolerant shrubs increased before and during early succession, but they then declined and were gradually replaced by shade-tolerant plants after canopy closure. Through thinning and natural pruning, understory vegetation can flourish again [45–47], but the rate of the increase in species diversity slows as the forest ages [48]. Without thinning, however, or with delayed thinning, the understory vegetation development of Chinese fir is delayed [49]. These findings are consistent with our results and our first hypothesis. These results also showed that the species composition and diversity of deadwood depended mainly on LCPs. The deadwood of LCPs in the TF included multiple shade-intolerant and shade-tolerant species, while the deadwood of LCPs in the MF was composed only of shade-tolerant species. Some studies suggest that a few shade-intolerant tree species could survive under a closed canopy [50]. In the TF, re-closure of the canopy may lead to the extirpation of several populations of LCPs. Secondary factors, including population density, tree size, spatial patterns and interspecific associations [2,17,39,51,52], may also have contributed to the formation of this deadwood.

In this study, all three deadwood statuses were observed in the TF, while only snags and fallen wood were found in the MF; this implies that thinning promotes deadwood status, which is consistent with hypothesis 2. The formation of broken wood is most likely attributable to damage to smaller trees caused by thinning activities, with the damaged trees subsequently dying due to decreased vitality [11,42]. Disease and pest insects are likely to occur only occasionally [5]. Since neither the MF nor TF in this study suffered from obvious natural disturbances during cultivation, the fallen wood that we observed is probably attributable to preexisting snags. The snags may fall due to gravity or external forces after the roots rot. Pieces of fallen wood were generally smaller than snags, which further supports this theory and is in line with the known dynamics of deadwood during community succession [34]. In plantations and natural forests, positive relationships
between stand age and the abundance and sizes of snags have also been observed [15].

The species diversity of snags in the MF and TF in this study was higher than that of
fallen wood, especially in the TF, which suggests that the accumulation of deadwood is
ongoing. To our knowledge, few studies have discussed species diversity in different stages
of deadwood formation. Major natural disasters often lead to large quantities of snags in
stands [16,53–55]. The absence of fallen wood from LCPs in the MF may be related to the
low quantity of deadwood inputs from LCPs, the early successional status of the MF, and
the rapid decomposition of coarse woody debris that occurs in wet and warm subtropical
environments [34].

In the MF, the majority of deadwood pieces were composed of relatively small Chinese
topographic factors showed little association with either the species identity or diversity
of deadwood. Regular, high-density planting patterns accelerate the establishment of a
closed forest canopy. Canopy-dominant species impose severe pressure on understory veg-
etation [7,51] and may delay the development of deadwood. Meanwhile, the canopy of the
MF remains relatively intact, and the understory environment is stable [23,42,56]; this may
reduce the influence of topographic factors. In this study, the MF had gentle topography,
and little effect on vegetation development at the stand or quadrat level. As mentioned
above, cultivation may reduce the influence of abiotic environmental factors, including
topography, on the development of deadwood populations, although the mechanism and
duration of this effect are not yet clear.

In the TF, elevation was the only variable that appeared to promote the formation of
deadwood populations differing in origin and status. In alpine regions, elevation increases
the intensity and duration of light beneath the forest canopy [17], which promotes the
regeneration and growth of diverse communities of shade-intolerant species after logging.
Some LCPs in such stands are numerous, spatially clumped, and susceptible to habitat
disturbance [34]. Therefore, elevation is more closely correlated with the regeneration of
LCPs than with PS, which supported our hypothesis 3. So far, only Huang et al. [3] have
analyzed the relationship between habitat and mixed Chinese fir–broadleaved forest at the
regional scale (Wuyi Mountain region, Fujian Province, China). These authors argued that
altitude significantly affects the diversity of plant communities in different habitats, which
strongly supports our results.

The TF supported areas of steep topography, which was not conducive to soil or
water conservation, or the survival of young trees. Steeper slopes in the TF were therefore
negatively correlated with deadwood. In particular, there is abundant rainfall in the study
area, and forest soils are exposed after tree felling, which could result in a reduction in
species diversity. Due to the relatively small spatial size of our plots, the aspect and
convexity of the TF changed only gradually (see Figure S1), and these variables had weak
relationships with deadwood. Generally, thinning alters specific environmental conditions
related to topographic factors (e.g., microclimate, soil nutrients, litter) [8,57,58], which in
turn affects the species composition and diversity of deadwood.

5. Conclusions

Converting plantations into uneven age forests containing many native tree species
has attracted widespread interest. Deadwood is the inevitable product of this transforma-
tion process. Increasing the quantity and quality of deadwood will improve plantation
ecosystem services and functioning. However, there is lack of understanding regarding
how to create additional deadwood during the process of conversion. In the mountainous
area of southern China, we achieved the near-natural conversion of Chinese fir plantations
through interplanting and light thinning. We found that cultivation practices directly
determined the status, quantity, and quality of deadwood. Interplanting resulted in a large
quantity of conspecific deadwood, and promoted a high basal area through interspecific
and intraspecific competition, which was beneficial in terms of nutrient concentrations
and carbon storage. Thinning changes stand structures and habitats, and enhances the species
diversity of deadwood; however, the deadwood basal area and carbon storage amounts are
small in the short term. Many forest birds, insects, and soil animals preferentially exploit deadwood, but stand conversion methods to promote community diversity require further study. Topography is an important environmental factor affecting the development of vegetation communities in mountainous areas, but its role in the cultivation of most plantations has been ignored. Our results suggest that in combination with topographic factors, thinning may influence the rate of deadwood formation. In future, combining natural processes with plantation cultivation may create more deadwood, and more conversion models; the dynamics of dead wood and its relationship to wildlife should be studied further. The results of this study are of great significance for assessing conversion and plantation management methods over long periods, as well as for determining optimal stand cultivation practices.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su15129214/s1. Figure S1: Plants of the mixed forest and thinned forest, Table S1: Species occurred in the MF and TF.

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