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The impacts of thinning on the fruiting of saprophytic fungi in *Cryptomeria japonica* plantations in central Taiwan

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ABSTRACT

Forest thinning is an important method for managing forests, changing forest structure, biological diversity and community. This study examined forest thinning effects on macrofungal diversity and the environmental factors affecting fruiting and community structure. Field surveys were conducted from 2006 to 2010 in 35-year-old *Cryptomeria japonica* plantations in central Taiwan. Thinning was completed in October 2007 and included control, 25% thinning, and 50% thinning treatments. Each treatment had four replications. Forest thinning and time affected macrofungal species richness observed but not abundance. Thinning influenced macrofungal community compositions; however, the difference between the two thinning intensities was not significant. The macrofungal community showed significant differences between communities of eastern and northern aspect. A redundancy analysis indicated that macrofungal communities in the *C. japonica* plantations were significantly affected by relative humidity, light, canopy cover, soil water content, soil temperature, soil pH value and soil texture. The fruiting of a dominant coral fungal species, *Scytinopogon* sp., was affected by thinning and light. The fruiting bodies of this species decreased in the 25% thinning plots and disappeared in 50% thinning plots in the first two years post-thinning, but were recorded in the third year post-thinning. After thinning, macrofungal species richness observed decreased, the community changed, and changes were associated with environmental conditions. Forest thinning decreased observable macrofungal diversity and changed the community structure, and these changes were associated with environmental variation after thinning.

1. Introduction

Species diversity is increasingly considered a key function of the ecosystem (Scherer-Lorenzen et al., 2005). In recent decades, biodiversity conservation has been increasingly considered when conducting forest management operations (Bengtsson et al., 2000; Lindenmayer and Franklin, 2002). Thinning, a common forest management technique, improves the growth of the remaining trees and enhances forest regeneration (Grant et al., 2007). Thinning is nevertheless a disturbance to organisms in forest ecosystems and affects biodiversity and ecosystem function (Bengtsson et al., 2000). Studies regarding the impact of silvicultural systems on diversity and community have recently grown in number (e.g. Bonet et al., 2012; Luoma et al., 2004; Pilz et al., 2006; Seiwa et al., 2012; Teste et al., 2012; Yamashita et al., 2014). There has been lots of attention paid to soil arthropods and bacteria, and most of these studies focus on forests in the temperate zone (Luoma et al., 2004; Meyer et al., 2005; Pilz et al., 2006).

Fungi, a major component of biodiversity, are essential for decomposition, nutrient cycling (Chapin et al., 2002; Tate, 1995) and nutrient transport (Delvasto et al., 2006; Tortora et al., 2007) in the forest ecosystem. High fungal diversity is essential to support the stability and resilience of the forest ecosystem (Perry et al., 1989). Factors influencing the fungal community included vegetation (Ferris et al., 2000), environmental factors (Tedersoo et al., 2011), climate changes (Kauserud et al., 2008) and disturbance (Bonet et al., 2012; Luoma et al., 2004; Seiwa et al., 2012; Teste et al., 2012). Fungal species with different environmental tolerances shift in abundance in response to changing environments.

Studies on the response of the macrofungal community to thinning in tropical areas were few (Brown et al., 2006; Lin et al., 2011),

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and most of the studies in tropical area (eg., Lin et al., 2011) fell short of the link of changing environments and macrofungal community. Thus, knowledge regarding the effects of disturbances on macrofungal diversity and community are important for evaluating the stability and resilience of a forest ecosystem.

There were about 45,000 ha of *Cryptomeria japonica* plantations in mountainous regions (Taiwan Forestry Bureau 1995) in Taiwan. This tree species was introduced from Japan in 1896 and was cultivated extensively for economic uses in 1911. The plantation forest in Taiwan entered the maturation stage. However, timbers of this tree species are no longer popular in Taiwan because of high cost and low economic values. Due to these reasons, a new management strategy to incorporate the needs of ecosystem functioning, recreation, conservation and educational purposes is developed. In order to provide science-based knowledge to developing a reasonable strategy, the large scale project to investigate the effect of different thinning practices in communities and ecosystem functions was conducted.

Macrofungi are major components of global biodiversity and control the rates of key ecosystem processes. Understanding how macrofungi respond to the disturbance caused by forest thinning is important for developing forest management strategies and biodiversity conservation. This study investigated the thinning effects on macrofungal diversity and community and identified environmental factors affecting fruiting by investigating the phenology, diversity, and abundance of macrofungi. In this context, there were three principle questions to answer. First, what is the effect of thinning on fungal diversity and community structure in the plantations? Second, what environmental factors affect the macrofungal community after thinning? Third, what are the dominant species and the thinning effect on their fruiting pattern? Potential indicator species for recovery of the environments from forest thinning were also investigated.

2. Materials and methods

2.1. Study site

The study site is located in Zen-Len area, Nantou County in central Taiwan. The site ranges from 23°28′N to 23°55′ latitude and from 120°48′E to 121°09′E longitude. Elevation ranges from 1300 to 1500 m. Average annual air temperature and rainfall recorded from nearby Sun Moon Lake Weather Station (23°53′N, 120°54′E) were 15.78 °C and 2628 mm, respectively. Most rainfall at this site occurs during the summer, from June to September. Some rainfall also occurs during the spring, from March to May; there is no obvious dry season. The natural vegetation in this area was clear-cut about 35 years previous to the start of the study and replanted with Japanese cedar, *C. japonica* (L.f.) D. Don. Two hundred and twenty-two species were classified to understory trees and shrubs, including 55 species of ferns, 138 species of dicotyledon and 27 species of monocotyledon. The dominant species are *Elatostemma lineolatum majus* and *Diplazium dilataum* (Hsieh, 2010).

2.2. Experimental design

Twelve 1-ha permanent plots (100 × 100 m) with northern and eastern aspects were established (Fig. 1a) for long-term monitoring of biodiversity dynamics. Plot 1 to 5 and plot 12 had an easterly aspect while plots 6 to 11 had a northerly aspect. The twelve plots were divided into three treatments of four plots, and each plot was randomly assigned a treatment of control, a 25% or a 50% thinning treatment (Fig. 1a). Each plot was divided into one hundred 10 × 10 m grids, using a theodolite. Thinning treatments consisted of tree removal in alternating quadrats as indicated in Fig. 1b. In treatment plots with 25% thinning, trees in one 10-m quadrat with each 20-m quadrat were cut, while in 50% thinning plots, trees in two 10-m quadrats with each 20-m quadrat were thinned (Fig. 1b). Thinning was performed during June to September of 2007. Average numbers of residual trees per plot (post-thinning) were 956 (control), 693 (25% thinning) and 476 (50% thinning) (I-Fan Sun, personal communication, September 23, 2009). The basal area in the control, 25% thinning and 50% thinning treatment before thinning was 58, 50.1 and 55.3 m^2/ha (Wang et al., 2010). After thinning, the basal area in the control, 25% thinning and 50% thinning treatment was 58, 43.1 and 24.9 m^2/ha (Wang et al., 2010). Only logged trunks with diameters >20 cm were removed from thinned plots for economic uses. Leaves, branches, and smaller trunks that were produced by thinning were left in the plots. To serve as a control for forest type, sampling plots were also established near the plantations in a natural broadleaf forest dominated by Lauraceae and Fagaceae.

2.3. Collection, identification and documentation of macrofungal species

In order to investigate macrofungal diversity and community in the plots, six 10-m diameter circular subplots were established in each plot (Fig. 1c). Mature fruiting bodies in the subplots and on the transect line between the subplots were investigated from August 2006 to October 2010 once every two months during the fruiting season (March to October). Macro-morphological features of fresh sporocarps, such as size, shape and color, the substrates they grew and their ecology were noted (Lodge and Cantrell, 1995). Morphological descriptions were compiled for each species to establish their identities. Sporocarp numbers, fruiting seasons and locations were also recorded. Voucher specimens of each species were photographed *in situ* and then collected. The macrofungi were dried at 40 °C for 1 or 2 days and preserved at the Department of Life Sciences, Tunghai University, Taiwan. Some collections were deposited in National Museum of Natural Science. To identify specimens, literatures including Chang et al. (2000), Chou and Chang (2005), Chou (2010), Corner (1950), Laessoe (1999), Ryvarden (1991), Tzean et al. (2010) were consulted.

2.4. Monitoring of environmental factors

The environmental factors in each study site plot, including temperature, water content, soil texture and pH, and temperature, relative humidity and light in the forest, were measured to identify the factors that influenced the differences in the macrofungal community. Hourly soil temperature was detected by T-type Thermocouple-type sensor (Omega Engineering Ltd., Stamford, USA) at soil depths of 10 and 20 cm. Soil water content was detected by a Soil Water Capacitance Probe (Sentek Pty Ltd., Stepney, SA, Australia) at depths of 10 and 20 cm and data were recorded every 15 min. A soil:water ratio of 1:5 was used for the measurement of soil pH. Air-dried soils (<2 mm) were suspended in distilled water and dispersed by ultrasonication for 10 min. Dispersed soils were separated into clay, silt and sand fractions by sedimentation and centrifugation for the soil texture analysis (Jackson, 1979; Gee and Bauder, 1986). Air temperature and relative humidity in the forest were monitored by data loggers (HOBO Pro Series data logger, Onset, Bourne, MA). The data logger was placed at a height of 1.5 m and data were recorded every 5 min. Incident, light photosynthetically active radiation (PAR) was measured and recorded at 5 min intervals at a height of 1.5 m with a quantum light sensor (LI-COR LI190SB-L Quantum Sensor, Lincoln, Nebraska, USA). We used the percentage of unthinned area to represent percent canopy cover. For example, the percentage canopy cover of the control

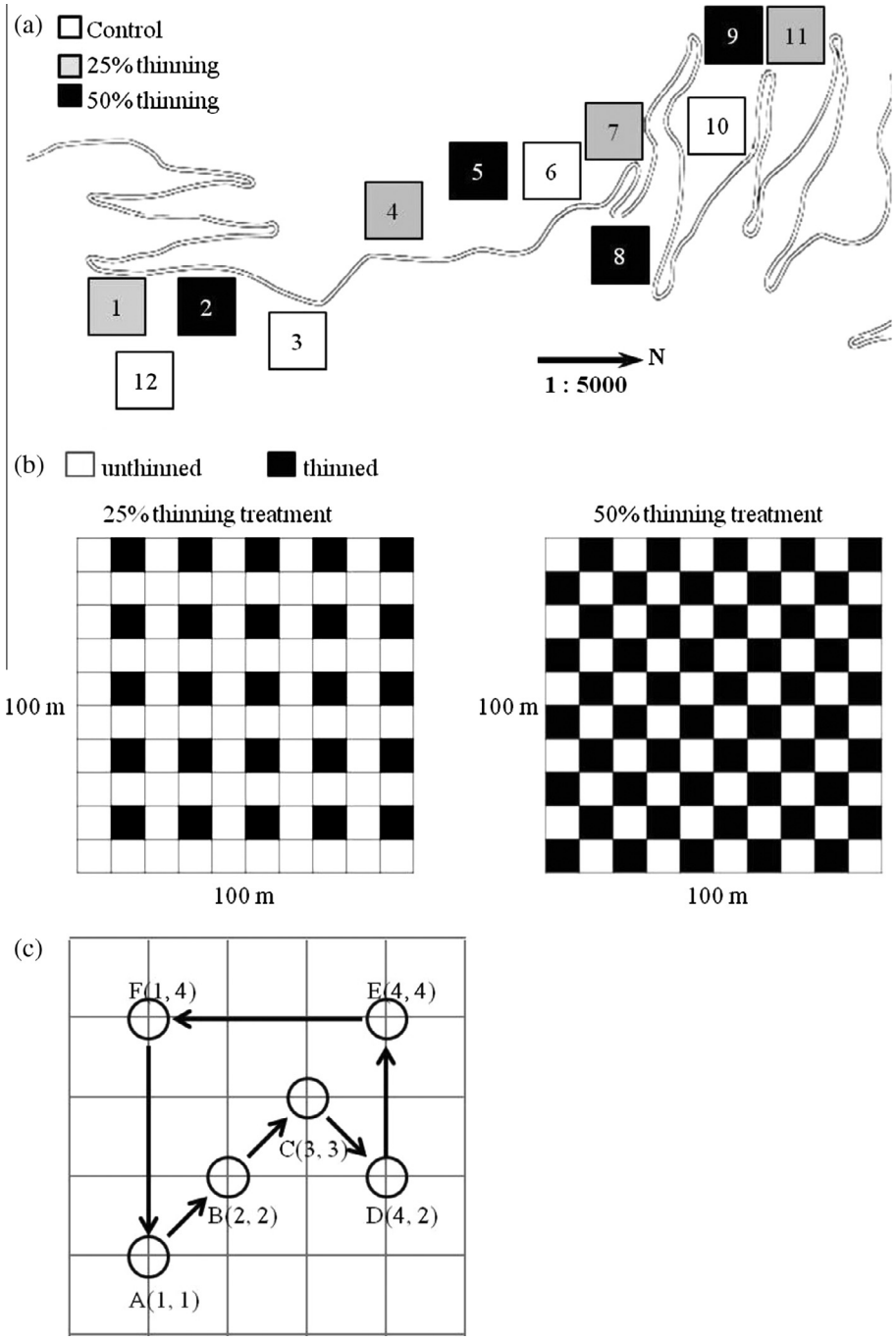

Fig. 1. Map of twelve plots, experimental design and investigated subplots in central Taiwan. (a) Twelve 1-ha plots (100 × 100 m) with three treatments (control and two thinning intensities) replicated four-fold and distributed in the plantations of Japanese cedar (*Cryptomeria japonica*) in central Taiwan; (b) thinned areas with plots corresponding to two thinning treatments are shown. The thinning treatments, including a 25% thinning treatment and a 50% thinning treatment, used the spacing thinning method. The plot was divided into 100 ten-meter grids. In the thinning treatment plots, trees in the dark ten-meter grids were thinned; (c) six 10-m diameter circular subplots and transect lines were located in each 1-ha plot. Circles refer to subplots and arrows refer to transect lines. Macrofungal diversity was investigated in these subplots and along the transect lines from August 2006 to October 2009.

plot, 25%-thinning plot and 50%-thinning plot was 100%, 75% and 50%, respectively.

2.5. Data analysis

Changes in fungal diversity and abundance over the course of the study were estimated by calculating the number of species and sporocarps and performing analysis of variance (ANOVA) using R software. Forest thinning and time series effects on diversity and abundance of different macrofungal functional groups were also analyzed by ANOVA.

Construction of a data matrix based on diversity and abundance of macrofungal morpho-species, which were identified to family level, was followed by square root transformations. The binary matrix was used to calculate Bray-Curtis Similarity (Clark and Warwick, 2001) and to construct nonparametric multi-dimensional scaling (MDS) plots using Primer 6 software (version 6. 1. 15; Primer-E Ltd., United Kingdom). The PERMANOVA plug-in

(version 1.0.5) of the Primer package was used to test observed differences statistically. A three-factor design permutational multivariate analysis of variance (PERMANOVA) was calculated with time, aspects and thinning treatments as the fixed factors to compare macrofungal community compositions over time. If there were significant differences for time, treatments, aspects or interactions, pairwise PERMANOVAs on the respective term for each level of the factor were performed on the respective term for each level of the factor. In all PERMANOVAs, a maximum of 999 random permutations was performed.

Redundancy analysis (Legendre and Anderson, 1999), as implemented in the "Vegan" package for R software (Oksanen et al., 2011) was used to analyze the relationships between environmental factors and macrofungal family profiles. Macrofungal family profiles were based on diversity and abundance and transformed by Hellinger distance (Rao, 1995). Air temperature, relative humidity, light, soil temperature and soil water contents were monitored as routine works every day. We only used the average data of sampling day and the data two weeks prior. The other environmental data, such as pH values and soil texture were monitored in each treatment. All the data were standardized and used to perform a redundancy analysis.

The abundance of dominant macrofungi was subjected by logarithmic transformation (base 10), and regression analysis was used to analyze the correlation between the abundance of dominant macrofungi and the environmental factors in plots by R.

3. Results

3.1. Macrofungal diversity

From August 2006 to October 2010, in twelve 1 ha plantation plots and a natural forest plot, a total of 158,037 fruiting bodies belonging to 610 taxa of macrofungi were observed and recorded. Among the bodies, 30% (184/610) of the taxa and 87% (138,079/158,037) of the fruiting bodies were identified to genus or species level, and 50 taxa were identified to family level. Although there were 376 unknown taxa, the majority of fruiting bodies were identifiable taxa. There were 376 unknown morpho-species accounting for only 10.77% of the fruiting bodies. In each plantation plot, 4–44 taxa and 26–42,986 sporocarps were recorded each year (Tables 1 and 2). Diversity of these macrofungi among plots varied greatly. In the natural forest plot, 34–66 taxa and 832–4531 sporocarps were found each year. The natural forest had higher species diversity.

Spring, summer and autumn were the main fruiting seasons. From August 2006 to June 2007, June and October had 103 and 18 macrofungal species, the highest and lowest species richness, respectively. Before thinning, the most fertile month was September. Most macrofungal species were recorded as low frequency. Four hundred and eighty-six species appeared only once, 53 species appeared twice. The species were complete turnover from year to year and plot to plot. *Scytinopogon* sp., *Oxyporus cunneatus*, *Lepiota cygnea*, and *Polyporus tenuiculus* were widespread species, and *Scytinopogon* sp., *O. cunneatus*, and *P. tenuiculus* were also dominant fruiting species at this site.

Compared with data before thinning, the number of fungal species observed decreased in all treatments in the first year post-thinning. This trend was also present in the second and third years post-thinning. In order to observe thinning and time series effects, ANOVA was used to determine whether species and sporocarp numbers changed over time and whether treatments differed over time. Species number changed through time ($F = 8.1422$; $P = 0.007$) and significantly decreased in thinning treatments ($F = 7.0178$; $P = 0.002$). Species richness was higher in control plots than in the 25% and 50% thinning plots ($P < 0.05$; Table 1). Species richness was significantly higher before thinning ($P < 0.05$; Table 1). The number of sporocarps increased slightly in all treatments in the 3 years post-thinning (Table 2). However, the number of sporocarps was not significantly different between thinning treatments ($F = 0.5003$; $P = 0.6$) or years ($F = 2.8544$; $P = 0.09$).

The relationship between fruiting fungal species richness and environmental factors was analyzed by multiple-regression. Relative humidity proved to be a good estimator of the species richness ($R^2 = 0.52$; Adjusted $R^2 = 0.35$). Regression analysis indicated that species richness was significantly and positively associated with relative humidity ($F = 3.124$; $P = 0.01$). Many macrofungal species was associated with higher relative humidity in the forest.

3.2. Functional groups of macrofungi

Tables 3 and 4 showed the diversity and abundance of saprotrophic macrofungi in the different treatments and time series. Saprotrophic macrofungi, including wood-inhabiting and soil-inhabiting, were dominant in the *C. japonica* plantations. Saprotrophs formed the main functional group of macrofungi in the *C. japonica* plantations.

Species richness of soil-inhabiting and wood-inhabiting saprotrophyic macrofungi observed in the plantations was significantly influenced by thinning ($F = 7.6820$; $P = 0.001$; $F = 5.1797$; $P = 0.01$). Richness and abundance of soil-inhabiting macrofungi were reduced by thinning but not influenced by time series. Control plots had significantly higher soil-inhabiting macrofungal species richness versus the 25%-thinning and 50%-thinning plots ($P = 0.001$; $P = 0.007$), but there was no difference between 25%-thinning and 50%-thinning plots ($P = 0.56$) (Table 3). Soil-inhabiting macrofungal abundance was significantly higher in control plots versus the 25%-thinning and 50%-thinning treatments ($P = 0.002$; $P = 0.010$) (Table 4). Species richness of wood-inhabiting macrofungi were decreased by thinning ($F = 5.1797$; $P < 0.0098$) and changed over time ($F = 13.9539$; $P < 0.0006$). The

Table 1
Number of macrofungal species in each plot in the *Cryptomeria japonica* plantations in Taiwan during investigated periods.

Time[a]	Control[b]					25% Thinning treatments					50% Thinning treatments					Natural forest
	P3[c]	P6	P10	P12	Means	P1	P4	P7	P11	Means	P2	P5	P8	P9	Means	
Before	41	32	16	30	30	17	28	31	24	25	29	44	28	29	33	66
1st yr	20	8	28	9	16	7	15	10	20	13	4	10	14	15	11	61
2nd yr	13	11	32	10	17	8	17	17	13	14	16	10	24	21	18	46
3rd yr	17	10	10	18	14	6	26	8	10	13	10	18	6	30	16	34

[a] Investigated periods, before: August 2006 to June 2007; 1st yr: 1st year post-thinning which is from March 2008 to October 2008; 2nd yr: 2nd year post-thinning which is from March 2009 to October 2009; 3rd yr: 3rd year post-thinning which is from March 2010 to October 2010.
[b] Treatments, including control, 25% thinning and 50% thinning treatments. Each treatment included four plots.
[c] Plot number.

Table 2
Number of macrofungal sporocarps in each plot in the *Cryptomeria japonica* plantations in Taiwan during investigated periods.

Time[a]	Control[b]					25% Thinning treatments					50% Thinning treatments					Natural forest
	P3[c]	P6	P10	P12	Means	P1	P4	P7	P11	Means	P2	P5	P8	P9	Means	
Before	1269	1067	344	837	879	227	553	3609	841	1308	1174	2309	529	1521	1383	832
1st yr	725	2204	1690	4762	2345	26	732	2755	5545	2265	250	98	3691	3144	1796	898
2nd yr	312	42986	6185	1576	12765	245	2563	2638	647	1523	484	77	10880	3867	3827	3545
3rd yr	2794	6678	3888	4725	4521	210	1029	2152	894	1071	141	746	1810	10,802	3375	4531

[a] Investigated periods, before: August 2006 to June 2007; 1st yr: 1st year post-thinning which is from March 2008 to October 2008; 2nd yr: 2nd year post-thinning which is from March 2009 to October 2009; 3rd yr: 3rd year post-thinning which is from March 2010 to October 2010.
[b] Treatments, including control, 25% thinning and 50% thinning treatments. Each treatment included four plots.
[c] Plot number.

Table 3
Number of saprotrophic species in each plot in the *Cryptomeria japonica* plantations in Taiwan during investigated periods.

Time[a]	Functional group[b]	Control[c]					25% Thinning treatments					50% Thinning treatments					Natural forest
		P3[d]	P6	P10	P12	Means	P1	P4	P7	P11	Means	P2	P5	P8	P9	<eans	
Before	SS	16	10	3	7	9	5	7	7	4	6	10	12	14	12	12	21
	WS	25	22	13	23	21	12	21	24	20	19	19	31	14	17	20	36
1st yr	SS	7	3	7	3	5	1	6	2	3	3	1	2	2	1	2	15
	WS	13	5	21	6	11	6	9	8	16	10	3	8	12	14	9	36
2nd yr	SS	7	5	17	3	8	4	7	5	6	6	5	4	5	3	4	9
	WS	6	6	15	7	9	4	10	11	7	8	11	6	19	16	13	32
3rd yr	SS	9	5	4	4	6	1	7	3	4	4	0	6	1	10	4	9
	WS	8	5	6	13	8	4	19	5	6	9	10	12	5	19	12	17

[a] Investigated periods, before: August 2006 to June 2007; 1st yr: 1st year post-thinning which is from March 2008 to October 2008; 2nd yr: 2nd year post-thinning which is from March 2009 to October 2009; 3rd yr: 3rd year post-thinning which is from March 2010 to October 2010.
[b] Ecological group, SS: soil-inhabiting saprotroph; WS: wood-inhabiting saprotroph.
[c] Treatments, including control, 25% thinning and 50% thinning treatments. Each treatment included four plots.
[d] Plot number.

Table 4
Number of saprotrophic sporocarps in each plot in the *Cryptomeria japonica* plantations in Taiwan during investigated periods.

Time[a]	Functional group[b]	Control[c]					25% Thinning treatments					50% Thinning treatments					Natural forest
		P3[d]	P6	P10	P12	Means	P1	P4	P7	P11	Means	P2	P5	P8	P9	Means	
Before	SS	113	797	157	124	298	46	40	949	167	301	62	59	165	270	139	339
	WS	1156	270	187	713	582	181	513	2660	674	1007	1112	2247	364	1251	1244	478
1st yr	SS	15	122	622	148	227	7	55	103	17	46	1	6	5	9	5	58
	WS	710	2082	1068	4614	2119	19	677	2652	5526	2219	249	92	3686	3135	1791	690
2nd yr	SS	19	755	535	97	352	77	82	123	77	90	17	11	43	62	33	17
	WS	293	42231	5650	1479	12,413	168	2481	2514	570	1433	467	66	10,837	3792	3791	3523
3rd yr	SS	27	414	394	15	213	2	113	28	94	59	0	13	1	34	12	44
	WS	2767	6264	3494	4580	4276	207	916	2124	800	1012	141	733	1809	10,767	3363	4445

[a] Investigated periods, before: August 2006 to June 2007; 1st yr: 1st year post-thinning which is from March 2008 to October 2008; 2nd yr: 2nd year post-thinning which is from March 2009 to October 2009; 3rd yr: 3rd year post-thinning which is from March 2010 to October 2010.
[B] Ecological group, SS: soil-inhabiting saprotroph; WS: wood-inhabiting saprotroph.
[c] Treatments, including control, 25% thinning and 50% thinning treatments. Each treatment included four plots.
[d] Plot number.

number of wood-inhabiting species was significantly lower in the 25%-thinning plots versus the control ($P = 0.03$) (Table 3). The number was also significantly higher post-thinning versus pre-thinning ($P < 0.05$) (Table 4).

The species and sporocarps of ectomycorrhizal fungi in the natural broadleaf forest were more abundant than in the plantations. Russulaceae and Amanitaceae were major ectomycorrhizal families in the natural broadleaf forest. However, natural forest had more saprophytic fruiting species than the plantation. Before thinning, the natural forest had 57 saprotrophic taxa and 9 ectomycorrhizal fungal species before thinning, while the control plots averaged 30 taxa (data not shown). The natural forest had almost twice the amount of saprophytic species.

3.3. Thinning influenced macrofungal community and environments

The macrofungal community based on morph-species profiles was influenced by the thinning treatments (Table 5). Multi-dimen-

Table 5
PERMANOVAs for the effects of time, aspect, thinning treatments and interactions on the macrofungal communities, based on macrofungal species and relative abundances in the *Cryptomeria japonica* plantations. A maximum of 999 permutations was possible.

Source	Degrees of freedom	Sum of squares	Pseudo-*F* ratio	Significance (*P*-value)
Year	3	29,375	3.9628	0.001
Thinning	2	7916	1.6018	0.034
Aspects	1	10,493	4.2467	0.001
Year × thinning	4	8593	0.86942	0.721
Year × aspects	3	10,597	1.4296	0.071
Thinning × aspects	2	6471	1.3094	0.127
Year × thinning × aspects	4	8308	0.84059	0.774
Residuals	26	64,242		
Total	45	154,980		

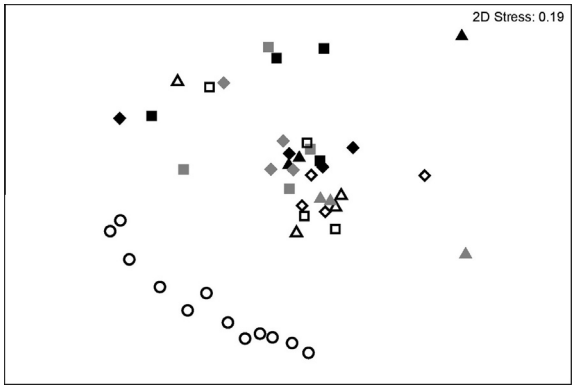

Fig. 2. Multi-dimensional scaling ordination of macrofungal communities from thinning treatments among years. Symbols represent years: circles, pre-thinning; triangles, first year post-thinning; squares, second year post-thinning; diamond, third year post-thinning. Colors represent thinning treatments: white, gray and black represented control, 25% thinning and 50% thinning plots, respectively.

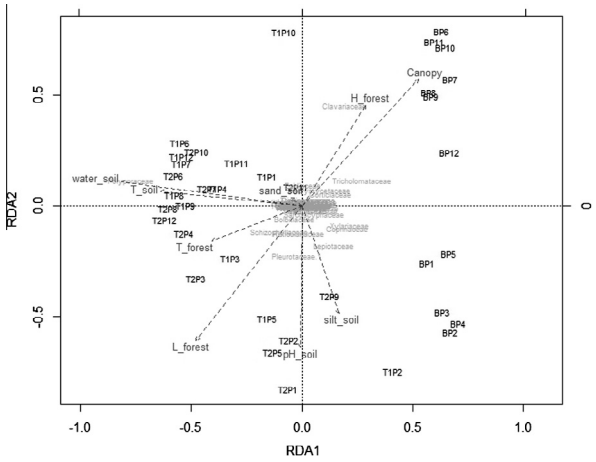

Fig. 3. Redundancy Analysis of macrofungal communities and environmental factors instudied twelve plots from August 2006 to October 2009. Black words refer to macrofungal communities from different years and plots. B: before thinning; T1: first year post-thinning; T2: second year post-thinning. P: number of plot. Gray and dashed arrows refer to environmental factors. T_forest: temperature in the forest; L_forest: light in the forest; water_soil: soil water content; T_soil: temperature in the soil; pH_soil: soil pH; H_soil: relative humidity in the soil. Light gray words refer to the macrofungal family.

sional scaling (MDS) plots showed that macrofungal communities in the 50%-thinning treatments were distinct from the communities in the control, but there was greater overlap area between the 25%-thinning and 50%-thinning treatments (Fig. 2). PERMANOVA pairwise comparisons also indicated that the macrofungal community from the 50%-thinning treatments was significantly different than that from control treatments ($P = 0.032$). There was no significant difference between other treatments and no interaction between years, aspects and thinning treatments (Table 5). The SIMPER test showed that *Oxyporus cuneatus* and *Scytinopogon* sp. were the main contributors of variation between the macrofungal communities in the control and 50%-thinning treatment, contributing 27.7% and 8.4% dissimilarity, respectively. The macrofungal species and abundance data matrix based on the family level were also used to test the effects of thinning levels on the macrofungal community. The same patterns were shown with the macrofungal community based on the level of morpho-species (data not shown).

To determine which environmental factors best explained the variation in macrofungal communities, we used redundancy analysis (RDA) to predict the principal coordinates (Fig. 3) using a linear combination of several environmental factors (Table 6). The arrows indicate the size and direction of the coefficients of the environmental variables in the linear model (Fig. 3). These environmental factors, including air temperature, relative humidity, light, canopy, soil water content, soil temperature, soil texture and pH, accounted for 38.37% of the variation of macrofungal communities. Relative humidity, light, canopy cover, soil water content, soil temperature, soil pH and soil texture (sand and silt) contributed significantly to explaining the variation in the macrofungal community (Fig 3; Table 7). Air temperature ($F = 12.73$; $P = 0.001$) and light ($F = 84.68$; $P < 0.001$) in the plantations significantly and negatively correlated with forest canopy cover. On the other hand, relative humidity ($F = 10.11$; $P = 0.003$) positively correlated with canopy cover.

3.4. Comparison of macrofungal species composition between investigated periods and aspects

A multi-dimensional scaling plot (Fig. 2) showed that prior to thinning, the macrofungal communities cluster together, separately from others. PERMANOVA showed that the macrofungal community responded to a time effect (Table. 5) and pairwise comparisons showed that the macrofungal community differed significantly among years (for all comparsions, $P < 0.01$).

Aspect markedly influenced the macrofungal community (Table 5). A multi-dimensional scaling plot generated from macrofungal morpho-species profiles showed that the macrofungal communities from northerly aspects clustered separately from those with easterly aspects (Fig. 4). *Scytinopogon* sp. was found only in plots with northerly aspects and *Oxyporus cuneatus* was more abundant in plots with northerly versus easterly aspects. The SIMPER test showed that *Oxyporus cuneatus* and *Scytinopogon* sp. was the main contributor, accounting for 28.6 and 8.9% of the variation in the macrofungal communities between the north and east aspects.

Table 6
Data corresponding to environmental variables used in redundancy analysis.

Time	Treatment	Temperature (°C)	Relative humidity (%)	Light (m mole/s m^2)	Canopy cover (%)	Soil water content (%)	Soil temperature (°C)	pH	Sand (%)	Silt (%)	Clay (%)
Before thinning[a]	Control[b]	17.77	97.28	2288.56	100	10.26	11.62	4.27	75.0	12.5	12.5
		17.79	97.15	1960.46	100	17.01	16.88	4.05	74.0	16.0	10.0
		17.78	96.96	1294.55	100	11.94	14.38	4.24	77.0	14.0	9.0
1st year post-thinning	Control	17.57	97.08	2987.00	100	20.29	16.98	4.27	75.0	12.5	12.5
	25%	17.77	95.85	7028.43	75	22.35	17.62	4.05	74.0	16.0	10.0
	50%	17.99	95.21	10,412.10	50	23.38	17.50	4.24	77.0	14.0	9.0
2nd year post-thinning	Control	18.12	97.19	2202.52	100	18.54	17.74	4.27	75.0	12.5	12.5
	25%	18.26	96.45	5253.19	75	20.23	18.33	4.05	74.0	16.0	10.0
	50%	18.48	95.90	9839.95	50	20.51	18.15	4.24	77.0	14.0	9.0

[a] Investigated periods, before thinning: August 2006 to June 2007; 1st year post-thinning: March 2008 to October 2008; 2nd year post-thinning: March 2009 to October 2009; 3rd year post-thinning: March 2010 to October 2010.
[b] Treatments, including control, 25% thinning and 50% thinning treatments. Each treatment included four plots.

Table 7
Results of redundancy analysis for influences of environmental factors on the macrofungal communities.

Environmental variables		r^2	Significance (*P*-value)
Temperature in forest		0.0935	0.223
Relative humidity		0.1627	0.040
Light		0.3255	0.002
Canopy		0.3227	0.002
Soil water contents		0.3522	0.001
Soil temperature		0.2135	0.016
Soil pH value		0.2593	0.012
Soil texture	Sand	0.0024	0.959
	Silt	0.1705	0.046
	Clay	0.4018	0.046

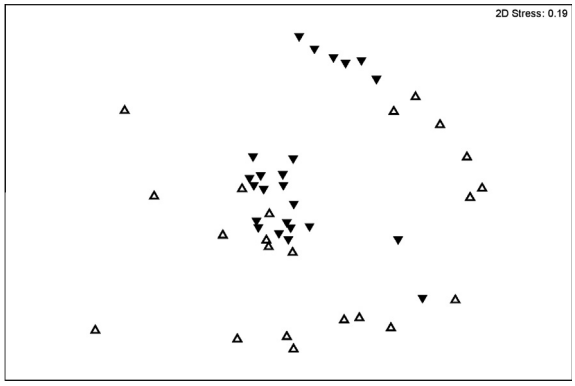

Fig. 4. Multi-dimensional scaling ordination of macrofungal communities from north and east aspects: triangles represented macrofungal communities in sampling plots; white inverted triangles, east aspect; black inverted triangles, north aspect.

3.5. Environments influenced fruiting patterns of widespread species

Four widespread macrofungal species showed different population fluctuations after thinning. The wood-habitant saprophytes *O. cunneatus* and *P. tenuiculus* seemed unaffected by thinning. *O. cunneatus* was widely distributed and fruited from March to October (Fig. 5a). After thinning, the abundance of *O. cunneatus* macrocarps increased in thinned plots (Fig. 5a); fruiting of *O. cunneatus* primarily correlated with light in the forest ($F = 15.8456$; $P = 0.0004$) and soil pH ($F = 5.7191$; $P = 0.002$). *P. tenuiculus* was distributed widely, except for plot 2 (50% thinning treatment), and the fruiting season was from March to October (Fig. 5b). Fruiting numbers of *P. tenniculus* were positively correlated with forest relative humidity ($F = 4.6644$; $P = 0.04$) and negatively associated with forest temperature ($F = 5.8923$; $P = 0.02$).

L. cygnea, a soil-habitant, is distributed widely and did not fruit in the first year post-thinning in three treatments until October 2008 (Fig. 5c). Its fruiting season was from March to October (Fig. 5c), and its abundance correlated with light levels ($F = 7.3225$; $P = 0.02$) and soil pH ($F = 7.9037$; $P = 0.01$). The abundance of *Scytinopogon* sp. macrocarps was clearly affected by thinning intensity (Fig. 5d). After thinning, the coral fungi fruited as before in the control plots, but declined in the plots which had 25% thinning and was not found at all in the plots with 50% thinning during the first and second years post-thinning (Fig. 5d). The fruiting of *Scytinopogon* sp. in 50%-thinned plots started to recover in the third year post-thinning and the abundance of its macrocarps was negatively correlated with thinning intensity ($F = 6.7844$; $P = 0.02$) and light levels ($F = 9.5173$; $P = 0.005$).

4. Discussion

Saprotrophic and symbiotic functional groups were recorded in this study. No ectomycorrhizal fungi have been reported as symbionts of *C. japonica*; the ectomycorrhizal fungi in the plantations were associated with other tree species, rather than *C. japonica*. Saprotrophic macrofungal diversity in the natural broadleaf forest was higher than in the conifer plantations examined in this study. It might due to the plant diversity of natural broadleaf forest was higher than the plantation (I-Fan Sun, personal communication, September 23, 2009). Higher vascular plant diversity supported higher macrofungal diversity (Packham et al., 2002).

With high frequency and comprehensive investigations in this study, we documented high diversity of saprophytic macrofungi. There were 4000 vascular plant species in Taiwan. Based on the 1:6 vascular plant–fungus ratio (Hawksworth, 1991), 25,000 fungi species were estimated (Tzean et al., 2010). About 6000 fungal species (24%) were documented (Tzean et al., 2010) in Taiwan. In our study, 30% fungal species which produced majority (87%) of fruiting bodies were identified. This is common for fungal surveys (Robinson and Tunsell, 2007; Robinson and Williams, 2011).

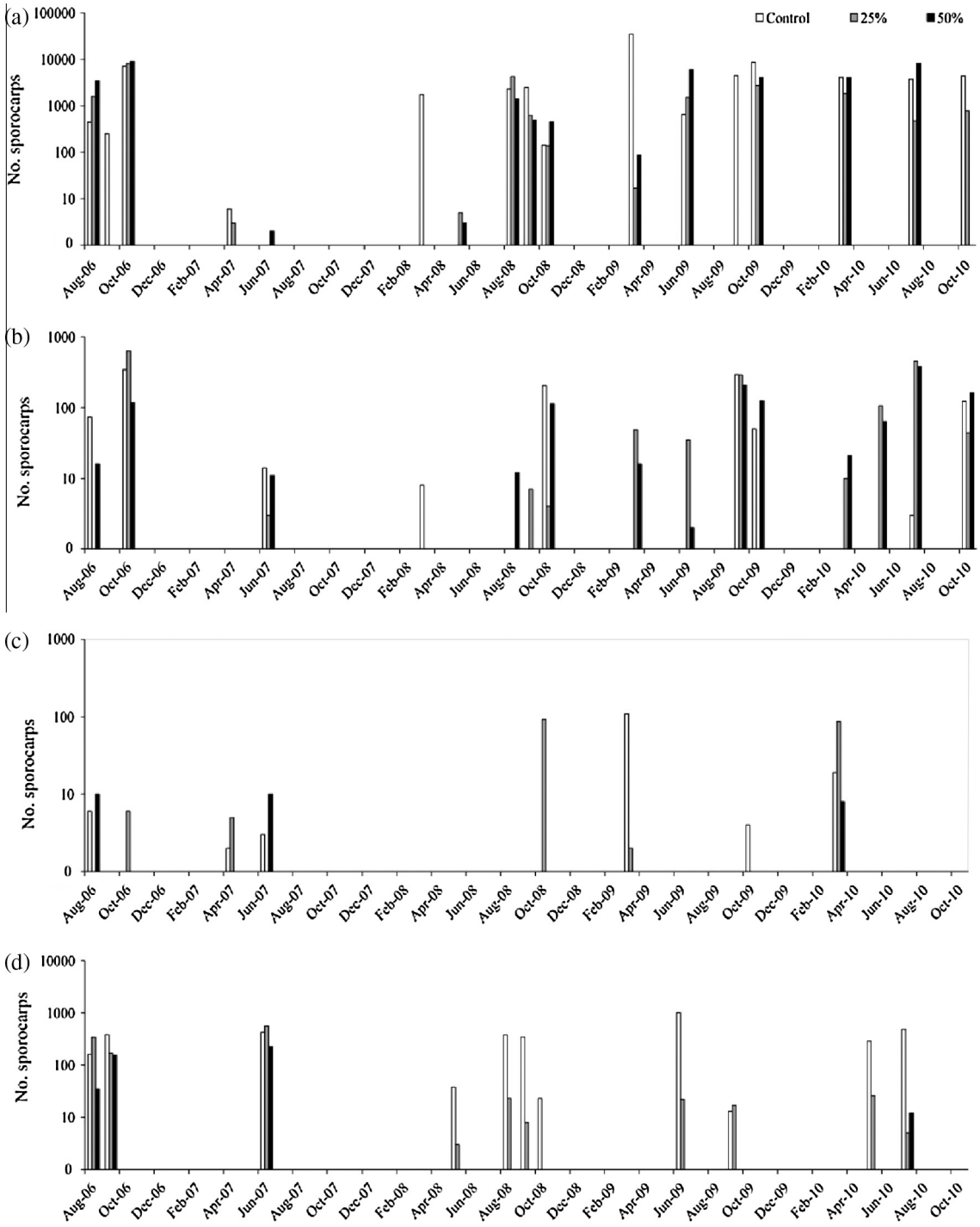

Fig. 5. The temporal fruiting pattern of *Oxyporus cunneatus* (a), *Polyporus tenuiculus* (b), *Lepiota cygnea* (c), and *Scytinopogon* sp. (d).

A forest thinning disturbance causes significant declines in the species richness of saprophytic macrofungi but does not affect sporocarp abundances. The great variations of fruiting number among plots within treatment could make it difficult to test thinning effects on abundance of saprotrophic fungi. This study also confirmed the negative effects of silvicultural practices on saprophytic fungal diversity and observed results similar to those of Müller et al. (2007a,b) and Kebli et al. (2012). The richness decline may be caused by the decrease of fruiting species or the disappearance of certain species.

Changes in environmental factors after thinning influenced fruiting species and fruiting patterns. For example, the fruiting of *L. cygnea* was influenced by light and soil pH, whereas the fruiting of *Scytinopogon* sp. was influenced by light and thinning intensity. Thinning not only changed the microenvironments, in our observation, the practices also disturbed the understory and soil surface which affected the fruiting of soil-inhabiting fungi. In the 50%-thinned plots, the population of *Scytinopogon* sp. disappeared after the thinning treatment. Ultimately, a small population of *Scytinopogon* sp. appeared at new sites during the third year post-thinning.

Both *L. cygnea* and *Scytinopogon* sp. were soil-inhabiting macrofungal species. Thinning practices disturb the soil surface, compact the soil, change forest environments and soil characters, and all of these factors influence macrofungal survival, vegetative growth, and fruiting, decreasing the richness and abundance of soil-inhabiting macrofungi.

Our results also confirm that thinning decreased the species richness of observed wood-inhabiting macrofungi (Sippola et al., 2001; Josefsson et al., 2010; Kebi et al., 2012). New stumps and wood produced by thinning are presumed to be habitats with little-to-no competition, resulting in a patchwork distribution of new wood-inhabiting macrofungi (pioneer species). The majority of wood-inhabiting macrofungi, like *P. tenniculus* and *O. cunneatus*, fruited massively in this niche. These species are able to undergo rapid fruit-body formation as soon as a suitable substrate was available. However, the vegetative growth of a minority of wood-inhabiting macrofungi continued for a long time until they occupied the substrate or after initial fruiting (Olsson et al., 2011; Otterson, 2013). The fact that these species were not recorded might be due to fruiting related to suboptimal conditions and/or the need for a long timeframe, or alternatively abundance subsided post-thinning. Although thinning provided extra substrates for wood-inhabiting fungi, the wood-inhabiting macrofungal richness was diminished in the thinned plots with disappearance of minor species and the delay of fruiting. Lohmus (2011) also found that the number of polypore species declined during the first 20 years after cutting, rebounding afterward. The post-harvest time interval should rank among the most important factors determining the species richness of wood-inhabiting macrofungi. In the context of various forest management methods, the recovery of diversity of wood-inhabiting macrofungi merits future study.

Macrofungal communities are often affected by forest management activities, including clear-cutting (Lindner et al., 2006) and selective logging (Bader et al., 1995; Yamashita et al., 2014), and the environmental changes have been suggested to be an important factor that determines the biodiversity and community (Eveling et al., 1990; Pererdo et al., 1983). Thinning has been reported to change the observed macrofungal community in *C. japonica* and *Chamaecyparis formosensis* plantations (Lin et al., 2011). In this study, 50% thinning treatments changed the macrofungal community, which was correlated with the alteration of environmental parameters, including relative humidity, light and canopy in the forest and water contents, temperature, soil pH and texture. It is presumed that thinning decreases plantation canopy cover, causing an increase in air temperature, a decrease in relative humidity and an increase of light in the forest. Changes in these environmental regimes influenced mushroom fruiting.

Aspect was also an important factor controlling fruiting conditions for individual species (Bonet et al., 2004). Aspect can have very significant influences on microclimates. For example, slopes with western or southern aspects are warmer and dryer than eastern or northern aspects in the northern hemisphere (Bennie et al., 2006). Bertling and Cowan (1998) reported that in the southern hemisphere, daylight intensity declined on eastern aspects and increased on northern aspects as austral autumn progressed. Light has comprehensive effects on the formation of basidiomycete and ascomycete fruiting bodies; for example, it determines whether the fruit bodies are produced, well as the development patterns (Morimoto and Oda, 1973) and numbers produced (Elliott, 1994; Moore et al., 2008). In this study, temperature and relative humidity were significantly higher in northerly aspects than in easterly aspects. Light was slightly higher in northerly aspects than in easterly aspects, although the difference was not significant. Moreover, aspect significantly influenced macrofungal community and *Scytinopogon* sp. distribution. Overall then, fruiting of macrofungi correlated with microclimates, which varied with aspect.

The temporal fluctuation in macrofungal communities is likely to be related to climatic variation (Matsuda and Hijii, 1998; Lagana‘ et al., 2002; Straatsma and Krisai-Greilhuber, 2003; Baptista et al., 2010) and macrofungal phenology. Annual rainfall in 2007 (before thinning), 2008 (the first year post-thinning), and 2009 (the second year post-thinning) in this study was 3540, 3177, and 1475 mm, respectively (http://www.cwb.gov.tw/V7/climate/dailyPrecipitation/dP.htm). Macrofungal communities in control plots fluctuated during the timeframe studied, possibly due to a variable weather conditions that included annual rainfall; the number of species found in this site varied with mean yearly rainfall. Weather parameters clearly play a major role, affecting the periodicity and fluctuations of communities.

Although molecular methods could detect more taxa than fruiting body survey, the sporocarp communities were similar with the most abundant OTUs by 454 pyrosequence (Kubartova et al., 2012). That means changes in sporocarp communities post-thinning could reflect the population dynamics of the most abundant fungal taxa. This study was relied on sporocarps observations and the results represent the effect on fruiting of the fruiting fungi. It reflects both the reproductive activity and absence. Moreover, the molecular methods (e.g., DGGE or next generation sequence) to confirm the observed trends and the genetic dynamics of dominant species population were worth of further investigation.

Currently in Taiwan, economic values of *C. japonica* plantation are no longer emphasized but their ecosystem functioning, recreation, conservation and educational values are incorporated in management purposes. Thinning had negative influences on observed macrofungal diversity. However, the gaps were created in the plantation forest post-thinning, seeds of native tree species (Fagaceae) from natural forest might be dispersal and colonize in plantation forest. As a consequence, the appearance of ectomycorrhizal fungi could be predicable. Our results show that 25% thinning treatment had fewer impacts on observed macrofungal community and it is a better management method than 50%-thinning or clear-cutting for biodiversity preservation.

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Appendix A. The identified soil- and wood-inhabiting fungi of the area

Ecological group	Scientific name	Ecological group	Scientific name	Ecological group	Scientific name	Ecological group	Scientific name	Ecological group	Scientific name
SS	*Agaricus praeclaresquamosus*	WS	*Pseudohydnum gelatinosum*	SS	*Lepiota* sp. 7	WS	*Trametes hirsuta*	WS	*Marasmiellus candidus*
SS	*Agaricus* sp.	SS	*Geastrum triplex*	SS	*Lepiota* sp. 8	WS	*Trametes versicolor*	WS	*Marasmiellus nigripes*
WS	*Auriclaria delicata*	WS	*Ascocoryne cylichnium*	SS	*Lepiota* sp. 9	WS	*Trichaptum biforme*	WS	*Marasmiellus ramealis*
WS	*Auricularia auricula*	SS	*Leotia lubrica*	SS	*Leucoagaricus bresadolae*	WS	*Tyromyces incarnatus*	WS	*Marasmius maximus*
WS	*Auricularia polytricha*	WS	*Elmerina cladophora*	SS	*Calvatia craniiformis*	WS	*Cymatoderma elegans*	WS	*Marasmius* sp. 1
SS	*Conocybe lactea*	SS	*Hygrocybe coccineocrenata*	SS	*Lycoperdaceae* sp.	SS	*Aleuria aurantia*	WS	*Marasmius* sp. 2
SS	*Scytinopogon* sp.	SS	*Hygrocybe* sp.	SS	*Lycoperdon perlatum*	WS	*Scutellinia scutellata*	WS	*Marasmius* sp. 3
WS	*Clavicorona pyxidata*	WS	*Hypocrea gelatinosa*	SS	*Dictyophora indusiata*	SS	*Ramaria stricta*	SS	*Mycena pura*
WS	*Coprinus disseminatus*	SS	*Lepiota acutesquamosa*	WS	*Steccherinum rhois*	WS	*Lycogala epidendrum*	WS	*Mycena* sp. 1
WS	*Coprinus micaceus*	SS	*Lepiota atrosquamulosa*	WS	*Lentinus edodes*	WS	*Cookeina insititia*	WS	*Mycena stylobates*
WS	*Coprinus* sp. 1	SS	*Lepiota cristata*	WS	*Panus fulvus*	WS	*Sarcoscypha coccinea*	WS	*Oudemansiella mucida*
WS	*Coprinus* sp. 2	SS	*Lepiota cygnea*	WS	*Pleurotus ostreatus*	WS	*Sarcoscypha humberiana*	WS	*Oudemansiella platyphylla*
SS	*Psathyrella candolleana*	SS	*Lepiota fusciceps*	WS	*Pleurotus* sp. 1	WS	*Galiella javanica*	WS	*Oudemansiella radicata*
SS	*Psathyrella* sp.	SS	*Lepiota praetervisa*	WS	*Pleurotus* sp. 2	WS	*Schizophyllum commune*	WS	*Oudemansiella* sp. 1
SS	*Psathyrella* sp. 1	SS	*Lepiota* sp. 1	WS	*Pluteus nigrofloccosus*	WS	*Dicephalospora rufocornea*	WS	*Oudemansiella* sp. 2
SS	*Psathyrella* sp. 2	SS	*Lepiota* sp. 10	WS	*Pluteus* sp. 1	WS	*Naematoloma fasciculare*	WS	*Oudemansiella* sp. 3
SS	*Psathyrella* sp. 3	SS	*Lepiota* sp. 11	SS	*Pluteus* sp. 2	WS	*Pholiots* sp.	WS	*Oudemansiella* sp. 4
SS	*Psathyrella velutina*	SS	*Lepiota* sp. 12	WS	*Antrodiella liebmannii*	SS	*Psilocybe cubensis*	WS	*Resupinatus trichotis*
WS	*Stereum ostrea*	SS	*Lepiota* sp. 13	WS	*Coriolopsis aspera*	WS	*Trichocoma paradoxa*	WS	*Xeromphalina campanella*
WS	*Xylobolus spectabilis*	SS	*Lepiota* sp. 14	WS	*Lenzites betulina*	SS	*Baeospora myosura*	WS	*Daldinia eschscholzii*
WS	*Galerina hypnorum*	SS	*Lepiota* sp. 15	WS	*Microporus affinis*	WS	*Campanella junghuhnii*	WS	*Daldinia* sp. 1
WS	*Galerina* sp.	SS	*Lepiota* sp. 16	WS	*Microporus xanthopus*	WS	*Collybia confluens*	WS	*Hypoxylon* sp. 1
WS	*Gymnopilus liquiritiae*	SS	*Lepiota* sp. 17	WS	*Oligoporus caesius*	SS	*Collybia* sp.	WS	*Hypoxylon* sp. 2
WS	*Gymnopilus* sp.	SS	*Lepiota* sp. 18	WS	*Oligoporus lowei*	WS	*Crinipellis stipitaria*	WS	*Xylaria allantoidea*
WS	*Gymnopilus* sp. 1	SS	*Lepiota* sp. 19	WS	*Oxyporus cunneatus*	WS	*Cyptotrama asprata*	WS	*Xylaria carpophila*
WS	*Gymnopilus* sp. 2	SS	*Lepiota* sp. 2	WS	*Polyporus arcularius*	WS	*Dictyopanus gloeocystidiatus*	WS	*Xylaria cubensis*
WS	*Crepidotus* sp. 1	SS	*Lepiota* sp. 20	WS	*Polyporus badius*	WS	*Filoboletus manipularis*	WS	*Xylaria melanaxis*
WS	*Crepidotus* sp. 2	SS	*Lepiota* sp. 3	WS	*Polyporus dictyporus*	WS	*Hohenbuehelia hobsoni*	WS	*Xylaria polymorpha*
WS	*Calocera cornea*	SS	*Lepiota* sp. 4	WS	*Polyporus tenuiculus*	WS	*Hohenbuehelia reniformis*	WS	*Xylaria* sp. 1
WS	*Calocera viscpsa*	SS	*Lepiota* sp. 5	WS	*Pycnoporus sanguineus*	SS	*Laccaria* sp. 1	WS	*Xylaria* sp. 2
WS	*Dacrymyces palmatus*	SS	*Lepiota* sp. 6	WS	*Skeletocutis stellae*	SS	*Laccaria* sp. 2	WS	*Xylaria* sp. 3

Ecological group, SS: soil-inhabiting saprotroph; WS: wood-inhabiting saprotrop.

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