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Drivers of macrofungal composition and distribution in Yulong Snow Mountain, southwest China

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Abstract

Although environmental factors strongly affect the distribution of macrofungi, few studies have so far addressed this issue. Therefore, to further our understanding of how macrofungi respond to changes in the environment, we investigated the diversityand community composition of fungi based on the presence of fruiting bodies in different environments along an elevation gradient in a subalpine Pine forest at Yulong Snow Mountain in southwest China. Two-hundred and twenty-eight specimens of macrofungi from twelve plots were identified using macro-morphological characteristics. We found that soil temperature had a significantly positive influence on total macrofungal and ectomycorrhizal species richness and diversity, while elevation gradients had a significantly negative influence. Furthermore, total macrofungal and ectomycorrhizal species community composition were significantly influenced by soil temperature and elevation gradients. No significant relationships were found between environment variables and the diversity and community composition of saprotrophic fungi in subalpine pine forest.

Keywords – ectomycorrhizal fungi – elevation gradient – soil temperature – species diversity – species richness

Introduction

Macrofungi are a crucial component of biodiversity essential for decomposition, carbon cycling, and nutrient transport in forest ecosystems (Hobbie et al. 1999, Lin et al. 2015).

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Macrofungi include either ascomycetes or basidiomycetes; all have large, easily observed sporocarps structures that form above or below ground (Gómez-Hernández et al. 2012). Based on estimates derived using plant/macrofungi species ratios, it has been suggested that there are between 53,000 and 110,000 species of macrofungi (Mueller et al. 2007). The two main functional groups of macrofungi are ectomycorrhizal fungi (ECM), with approximately 6,000 species, and saprotrophic fungi (Johnson et al. 2005).

Environmental factors such as precipitation, temperature, humidity, soil nutrient availability and plant species have been put forward as the primary factors responsible for differences in macrofungal species richness and community composition (Hillebrand 2004, Lentendu et al. 2011, Bahram et al. 2012, Singh et al. 2012, Tedersoo et al. 2014). There is some evidence that precipitation and temperature, coupled with plant diversity, are the key determinants of macrofungal distributions (Büntgen et al. 2011, Tedersoo et al. 2014). Changes in soil properties and climate parameters can directly influence the biodiversity and species composition ofassociated landscapes, and have been the focus of numerous studies looking at various organisms including fungi (Shi et al. 2014, Tello et al. 2015). However, despite these studies, many questions relating to the distribution of macrofungi and the drivers behind these distribution patterns remain unanswered (Baptista et al. 2010, Singh et al. 2012, van der Heijden et al. 2015).

This paper presents an assessment of the macrofungi recorded in 12 plots across a subalpine pine forest on the slopes of Yulong Snow Mountain in southwest China. We characterized macrofungal species diversity and communities to elucidate the effect of abiotic factors on fungal distribution. The aims of the study were to determine which environmental factors drive macrofungal species diversity and community composition, and their distribution in a subalpine pine forest. We hypothesize that macrofungal diversity is influenced by environmental factors such as soil temperature and elevation. Furthermore, we predict that macrofungal species richness, diversity, and community composition, decline with increasing elevation.

Materials & methods

Study site

The study area is located on the slopes of Yulong Snow Mountain, which is located in Lijiang County, southwest China, and which reaches 5,596 m above sea level (m.a.s.l.) at its highest point (Chang et al. 2014). The climate in this region experiences a summer monsoon wet season, lasting from May to October, and is dominated by the Qinghai-Tibetan Plateau circulation and westerly winds in the dry season, which lasts from November to April (Du et al. 2013). Mean annual temperature is around 10.3 °C, while the mean annual precipitation is 786.5 mm. The vegetation type for the study area is classified as subalpine coniferous forestand is dominated by coniferous species such as *Pinus armandii* and *Pinus yunnanensis* (Table 1), and some broad leaf trees such as *Quercus senescens* and *Rhododendron decorum*. The coniferous forest covering the study sites is about 45 years old, with a low level of disturbance.

The study sites were established in the Lijiang subalpine Botanical Garden (27°00′ N, 100°11′ E; 2830 m.a.s.l.) at four elevation points, ranging from 2,700 to 3,400 m.a.s.l. and consisting of 12 plots, three replicate plots at least 50 m apart were established at each elevation (Table 1). The sites were located in a continuous band of mixed *Pinus* forest. The main plants were identified by Yahuang Luo of the Kunming Institute of Botany, China. Replicate plots were established for each elevation point along the gradient. Soil temperature and humidity (10 cm depth)

Table 1 Description of the sites selected in the Lijiang Botanical Gardens, on the slopes of Yulong Snow Mountain, Lijiang County, China. Sites were covered in a continuous band of Pine forest, and were selected along an elevation gradient ranging from 2700 m.a.s.l to 3400 m.a.s.l. The climatic conditions were measured throughout the collecting season at each of the sites.

Replicate	Elevation (m.a.s.l.)	Coordinate	Dominant vegetation	MAT	MAW	ST
1	2718	27º0'0.01"N, 100º11'0.92"E	*P. yunnanensis* and *P. armandii*	15.13	98.59	16.23
2	2752	26º59'0.99"N, 100º11'0.83"E	*P. yunnanensis* and *P. armandii*			
3	2785	26º59'0.98"N, 100º11'0.74"E	*P. yunnanensis* and *P. armandii*			
1	2917	27º0'0.18"N, 100º11'0.58"E	*P. yunnanensis* and *P. armandii*	13.85	97.10	14.62
2	2964	27º0'0.21"N, 100º11'0.55"E	*P. yunnanensis* and *P. armandii*			
3	2987	27º0'0.24"N, 100º11'0.56"E	*P. yunnanensis* and *P. armandii*			
1	3185	28º0'0.33"N, 100º10'0.95"E	*P. yunnanensis* and *P. armandii*	12.41	89.94	16.37
2	3224	27º0'0.13"N, 100º10'0.99"E	*P. yunnanensis* and *P. armandii*			
3	3257	27º0'0.33"N, 100º11'0.17"E	*P. yunnanensis* and *P. armandii*			
1	3346	27º0'0.02"N, 100º10'0.69"E	*P. yunnanensis* and *P. armandii*	12.24	97.05	13.38
2	3376	27º0'0.21"N, 100º10'0.73"E	*P. yunnanensis* and *P. armandii*			
3	3343	27º0'0.21"N, 100º10'0.76"E	*P. yunnanensis* and *P. armandii*			

were recorded using HOBO Tidbit RG3-Mduration of the season (Luo et al. 2016). Air temperature and humidity were recorded in the plots duration of the rainy season, using a Vaisala MAWS 300. Canopy cover was estimated according to the method described by Sysouphanthong et al. (2010).

Macrofungal sampling

Macrofungal sporocarp sampling was conducted from July to September 2014. Every plot was surveyed once per week for a total of 14 visits across all plots. All aboveground macrofungal fruiting bodies in the 12 plots were collected and wrapped in aluminum foil, before being taken to the field station where macro-morphological characteristics were recorded and sporocarp dried in a food drier at 35 ℃. The dried macrofungal samples were sealed in Ziplock plastic bags for further morphological characterization. Based on the macro-characteristics, and with the aid of mushroom guide books, papers and online resources (http://www.indexfungorum.org/, http://mushroomexpert.com/, Lincoff 2000, Kendrick 2000, Hall et al. 2003), the collected specimens were identified to species. The taxonomic classification of species was based on the Index Fungorum (2016), which was used as the nomenclatural source. In addition, all macrofungi were grouped as either ectomycorrhizal, parasitic or saprotrophic fungi, based on mode of nutrition. The collected specimens were registered and deposited in the herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences.

Statistical analyses

All statistical analyses were performed in the *vegan* and *MASS* packages in *R* (R 3.1.2) (Dixon 2003). Species richness within each plot was quantified as the total community. Alpha-diversity was expressed as species diversity at each elevation gradient using the Shannon diversity index (H) (Shannon & Weaver 2015). The beta-diversity index was used to compare the difference in macrofungal species diversity between two locations using the Bray-Curtis and the Sorenson pair-wise dissimilarity matrix in *Betapart* package; multivariate analysis of variance of between elevations was used to examine the significancebased on beta diversity using the Arrhenius model. Pearson correlation was used to examine the correlations between species richness and environment variables, using OriginPro 8.5 to draw figures.

Species community composition between locations was displayed using non-metric multidimensional scaling (NMDS) ordination of Bray-Curtis similarity matrices and the function *metaMDS* in the *vegan* package (Dixon 2003). Relationships between environmental variables and macrofungal species community composition were tested using Procrustes correlation analysis and, NMDS ordinations, and the statistical significance of the analysis was assessed by the Monte Carlo procedure with permutations (999) in the vegan and MASS package.

Results

Collections

A total of 228 specimens of macrofungi, representing 103 species (Table 2), taxa 39 genera and 23 families were collected from 12 plots during the period of July to the end of September 2014. Of these, 71 species belonging to 20 genera were ectomycorrhizal fungi, while 32 species belonging to 19 genera were saprobes.

Macrofungal species richness and diversity

A comparison of the macrofungal species richness and alpha diversity along the elevation gradient indicated a negative correlation between species richness and increasing elevation (Table 3). Also, the diversity of ectomycorrhizal (ECM) fungi was significantly negatively correlated with elevation (P<0.05) (Table 4), whereassaprotrophic fungal diversity was not significantly affected by elevation. The highest levels of species richness and diversity were recorded at the lowest elevation (2,700–2,800 m.a.s.l). The lowest levels of species richnessand diversitywere observed at the highest elevation (3,300–3,400 m.a.s.l). Total macrofungal species richness and diversity were significantly positively correlated with ectomycorrhizal species richness (R^2=0.854, P<0.001) and diversity (R^2=0.846, P<0.001) (Fig. 1).

Total macrofungal species diversity was significantly positively correlated with air temperature (P<0.05) (Table 4). Furthermore, ECM species diversity was significantly positively correlated with air temperature (P<0.05) where as saprotrophic fungi showed no significant relationship with these variables (Table 4). Correlation analysis between macrofungal species richness and environmental variables showed that soil temperature was significantly positively correlated with total macrofungal and ECM fungal species richness (Table 4).

The correlation between the beta-diversity matrix and environmental variation indicated that total macrofungal and ECM species beta-diversity were significantly affected by elevation ($P<0.05$) (Table 5). There were also significant differences in the total macrofungal and ECM fungal species diversity among the following elevation bands, 2,700–2,800 and 2,900–3,000 m.a.s.l.; 2,700–2,800 and 3,300–3,400 m.a.s.l.; and 2,900–3,000 and 3,300–3,400 m.a.s.l. (P<0.01) (Table5), while there was no significant difference in saprotrophic fungal species diversity along the elevation gradient.

Table 2 Macrofungi found in the respective plots used in the study on Yulong Snow Mountain, southwestern China. Each macrofungi specimen is listed according to the elevation band in which it was collected.

Species name	Family	Elevation (m.a.s.l.)	Species name	Family	Elevation (m.a.s.l.)
Agaricus sp1	Agaricaceae	2,700–2,800	*Lactarius sphagneti*	Russulaceae	3,100–3,200; 3,300–3,400
Agaricus sp2	Agaricaceae	2,700–2,800	*Lactarius sp4*	Russulaceae	3,300–3,400
Agaricus fissuratus	Agaricaceae	2,700–2,800	*Lactarius torminosus*	Russulaceae	2,900–3,000
Agaricus semotus	Agaricaceae	3,100–3,200	*Lactarius volemus*	Russulaceae	3,100–3,200
Amanita caesarea	Amanitceae	2,900–3,000	*Lactarius xanthogalactus*	Russulaceae	2,700–2,800
Amanita gemmata	Amanitceae	2,700–2,800	*Lepista flaccida*	Agaricaceae	2,700–2,800
Amanita sp1	Amanitceae	2,900–3,000	*Lycoperdon perlatum*	Agaricaceae	2,900–3,000; 3,300–3,400
Amanita sp2	Amanitceae	3,100–3,200	*Marasmius oreades*	Marasmiaceae	3,300–3,400
Amanita porphyria	Amanitceae	2,700–2,800	*Marasmius undatus*	Marasmiaceae	3,100–3,200; 2,900–3,000
Amanita submembranacea	Amanitceae	2,900–3,000	*Melanoleuca cognata*	Tricholomataceae	3,300–3,400
Amanita vaginata	Amanitceae	2,700–2,800; 2,900–3,000; 3,100–3,200	*Mycena galericulata*	Mycenaceae	3,100–3,200
Boletopsis grisea	Bankeraceae	3,300–3,400	*Mycena sp 1*	Mycenaceae	2,900–3,000
Boletus edulis	Boletaceae	3,100–3,200	*Mycoleptodonoidesai tchisonii*	Meruliaceae	3,100–3,200
Boletus sp1	Boletaceae	2,700–2,800; 2,900–3,000	*Otidea leporina*	Pyronemataceae	2,700–2,800
Calvatia sp1	Agaricaceae	3,300–3,400	*Oudemansiella sp 1*	Physalacriaceae	2,700–2,800
Clitocybe bresadoliana	Tricholomataceae	2,900–3,000	*Pholiota aurivella*	Strophariaceae	2,900–3,000
Clitocybe infundibuliformis	Tricholomataceae	2,900–3,000	*Pholiota flammans*	Strophariaceae	2,900–3,000
Collybiaasema	Tricholomataceae	3,100–3,200	*Pseudohydnum gelatinosum*	Auriculariales	3,100–3,200
Collybia butyracea	Tricholomataceae	2,700–2,800; 3,100–3,200; 3,300–3,400	*Pulverobletus ravenelii*	Boletaceae	3,100–3,200
Collybia cirrhata	Tricholomataceae	2,700–2,800	*Pulveroboletus retipes*	Boletaceae	2,700–2,800
Collybia dryophila	Tricholomataceae	3,100–3,200; 3,300–3,400	*Ramaria sp1*	Gomphaceae	2,700–2,800
Collybia tuberosa	Tricholomataceae	3,100–3,200	*Ramaria stricta*	Gomphaceae	2,700–2,800
Cortinarius privignoides	Cortinariaceae	2,900–3,000	*Russula amoena*	Russulaceae	2,700–2,800; 2,900–3,000; 3,100–3,200
Cortinarius sp 1	Cortinariaceae	2,700–2,800	*Russula atropurpurea*	Russulaceae	2,700–2,800; 3,100–3,200
Cyathus sp2	Agaricaceae	3,100–3,200	*Russula brevipes*	Russulaceae	2,700–2,800; 3,100–3,200
Cyathus striatus	Agaricaceae	2,700–2,800; 2,900–3,000; 3,300–3,400	*Russula cremoricolor*	Russulaceae	3,100–3,200
Gomphus floccosus	Gomphaceae	3,300–3,400	*Russula cyanoxantha*	Russulaceae	3,100–3,200
Helvella crispa	Helvellaceae	2,700–2,800	*Russula emetica*	Russulaceae	2,700–2,800; 3,100–3,200
Helvella sp 1	Helvellaceae	2,700–2,800	*Russula faustiana*	Russulaceae	2,700–2,800

Species name	Family	Elevation (m.a.s.l.)	Species name	Family	Elevation (m.a.s.l.)
Hydnumum bilicatum	Hydnaceae	2,700–2,800	*Russula mustelina*	Russulaceae	3,100–3,200
Hygrocybe psittacina	Hygrophoraceae	3,300–3,400	*Russula ochroleuca*	Russulaceae	2,700–2,800; 2,900–3,000; 3,300–3,400
Hygrocybe reidii	Hygrophoraceae	2,700–2,800; 2,900–3,000	*Russula parazurea*	Russulaceae	3,100–3,200; 3,300–3,400
Hygrocybe sp 1	Hygrophoraceae	2,700–2,800; 2,900–3,000; 3,100–3,200; 3,300–3,400	*Russula queletii*	Russulaceae	3,100–3,200
Hygrophorus erubescens	Hygrophoraceae	2,700–2,800; 3,100–3,200	*Russula rosacea*	Russulaceae	3,100–3,200; 3,300–3,400
Hygrophorus latitabundus	Hygrophoraceae	2,700–2,800; 3,100–3,200	*Russula rosea*	Russulaceae	2,900–3,000; 3,100–3,200; 3,300–3,400
Hygrophorus russula	Hygrophoraceae	2,900–3,000	*Russula sp1*	Russulaceae	2,900–3,000
Hygrophorus tennesseensis	Hygrophoraceae	2,900–3,000	*Russula sp2*	Russulaceae	2,700–2,800; 3,100–3,200; 3,300–3,400
Hypholoma capnoides	Strophariaceae	2,900–3,000	*Russula undulata*	Russulaceae	2,700–2,800; 3,100–3,200
Inocybe rimosa	Inocybaceae	3,100–3,200	*Russula xerampelina*	Russulaceae	2,700–2,800; 2,900–3,000; 3,100–3,200; 3,300–3,400
Inocybe sp 1	Inocybaceae	2,700–2,800; 3,100–3,200	*Strobilomyces confusus*	Boletaceae	3,100–3,200
Laccaria bicolor	Hydnangiaceae	2,700–2,800	*Suillus bovinus*	Suillaceae	2,700–2,800; 3,100–3,200
Laccaria longipes	Hydnangiaceae	2,900–3,000; 3,300–3,400	*Suillus granulatus*	Suillaceae	2,700–2,800; 2,900–3,000; 3,100–3,200
Laccaria purpureobadia	Hydnangiaceae	3,300–3,400	*Suillus occidentalis*	Suillaceae	2,700–2,800
Laccaria sp 1	Hydnangiaceae	2,900–3,000	*Suillus pictus*	Suillaceae	2,900–3,000
Lactarius deliciosus	Russulaceae	2,700–2,800; 2,900–3,000; 3,300–3,400	*Suillus pinetorum*	Suillaceae	2,700–2,800; 2,900–3,000
Lactarius sp1	Russulaceae	3,100–3,200	*Suillus sp1*	Boletaceae	2,700–2,800; 3,300–3,400
Lactarius controversus	Russulaceae	2,900–3,000; 3,300–3,400	*Tricholoma scalpturatum*	Tricholomataceae	3,100–3,200; 3,300–3,400
Lactarius sp 2	Russulaceae	3,100–3,200	*Tylopilus sp1*	Boletaceae	3,100–3,200
Lactarius fuliginosus	Russulaceae	2,900–3,000; 3,100–3,200; 3,300–3,400	*Tylopilus intermedius*	Boletaceae	3,300–3,400
Lactarius rubidus	Russulaceae	3,100–3,200	*Xerocomus ripariellus*	Boletaceae	2,700–2,800
Lactarius sp3	Russulaceae	2,900–3,000	*Xerulara dicata*	Physalacriaceae	2,900–3,000
Lactarius sanguifluus	Russulaceae	3,100–3,200; 3,300–3,400			

Table 3 The total macrofungal, ECM and saprotrophic fungal species richness and diversity calculated for each of the plots along the elevation gradient. Diversity was estimatedby using the Shannon diversity index (H).

Elevation (m.a.s.l.)	**Richness**			**Shannon index (H)**		
	Total macrofungi	ECM fungi	Saprotrophic fungi	Total macrofungi	ECM fungi	Saprotrophic fungi
2700–2800	19.67±1.15	13.00±1.73	5.67±1.15	2.89±0.10	2.44±0.20	1.71±0.21
2900–3000	14.33±4.73	11.00±4.36	5.00±1.41	2.83±0.15	2.32±0.38	1.57±0.26
3100–3200	18.67±9.07	12.33±5.53	5.33±1.44	2.62±0.60	2.37±0.92	1.44±0.73
3300–3400	9.40±4.51	7.67±5.06	3.00±1.06	2.26±0.53	1.87±1.06	1.06±0.35

Species richness and Shannon index (H) had no significant difference between any two site's elevation gradients using Multivariate Analysis of Variance.

Table 4 Correlation analysis between environmental variation and total macrofungal, ECM and saprotrophic fungal species diversity (H) and community composition from different plots along the elevation gradient used in the study.

EF	Total macrofungi				ECM fungi				Saprotrophic fungi			
	H		CC		H		CC		H		CC	
	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
ELE	**-**0.401	**0.027***	0.809	**0.003****	**-**0.430	**0.021***	0.425	0.085	-0.293	0.085	0.206	0.404
AT	0.343	**0.045***	0.855	**0.001****	0.311	**0.059***	0.349	0.147	0.228	0.137	0.135	0.576
AH	0.050	0.485	0.335	0.159	-0.000	0.951	0.060	0.753	0.004	0.844	0.078	0.700
ST	0.127	0.254	0.441	0.071	0.430	**0.020***	0.608	**0.020***	0.205	0.161	0.338	0.188
CON	0.008	0.785	0.540	**0.030***	-0.043	0.517	0.651	**0.005****	-0.011	0.760	0.074	0.735

Permutation multivariate analysis of variance based on species diversity index. A maximum of 999 Monte Carlo permutations was possible. Pearson correlation test and significance was used to estimate the correlation between the ordinations. *ELE*: elevation; *AT*: air temperature; *AH*: air humidity; *ST*: soil temperature; *CON*: the percentage of canopy cover; *CC*: community composition; *H*: Shannon diversity index. $P<0.01$ ** $P<0.05$ *

Table 5 The total macrofungal and ECM fungal species beta diversity between different plots along the elevation gradient using the Bray-Curtis and the Sorenson pair-wise dissimilarity matrix.

Elevation (m.a.s.l.)	**Total macrofungi**		**ECM fungi**	
	R^2	*P*	R^2	*P*
2,700–2,800 & 2,900–3,000	0.282	0.005**	0.308	0.005**
2,700–2,800 & 3,100–3,200	0.224	0.184	0.194	0.532
2,700–2,800 & 3,300–3,400	0.369	0.005**	0.419	0.005**
2,900–3,000 & 3,100–3,200	0.237	0.303	0.223	0.154
2,900–3,000 & 3,300–3,400	0.271	0.005 **	0.328	0.005**
3,100–3,200 & 3,300–3,400	0.210	0.189	0.201	0.477

Permutation multivariate analysis of variance was used to calculate the significances levels between elevations based on the beta diversity of species using Arrhenius model. Significance levels were shown with asymmetric 95% confidence intervals. $P<0.01$ ** $P<0.05$ *

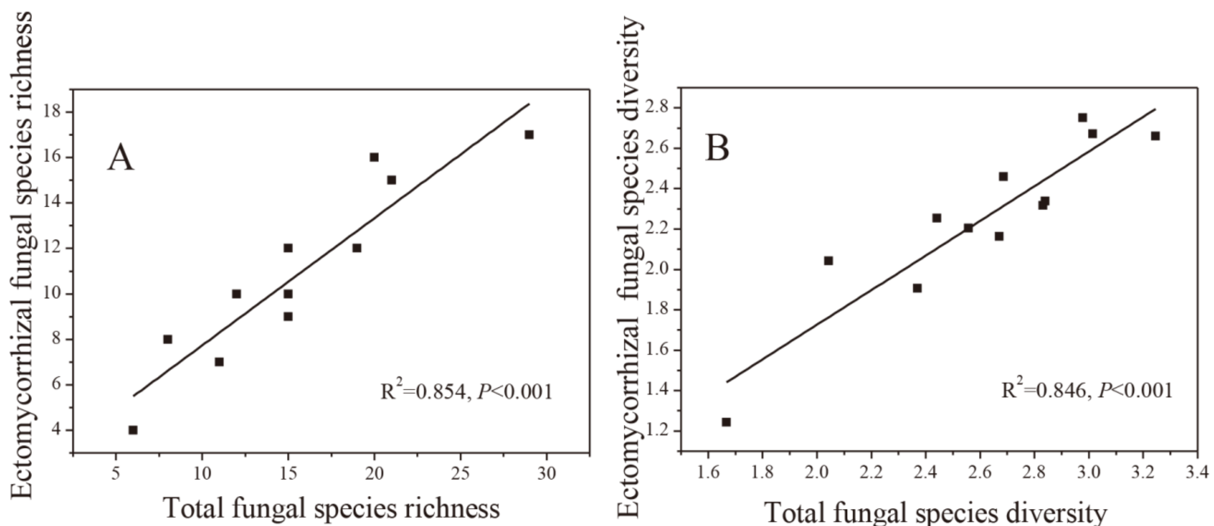

Fig. 1 – Correlation between total macrofungal and ECM fungal species richness (A), and between total macrofungal and ECM fungal species diversity (B). A linear model was selected to describe the relationships between total and ECM fungal species diversity and, between total and ECM fungal species richness. Significance level is shown with asymmetric 95% confidence.

Macrofungal species community composition and relative abundance

Macrofungal species community composition was significantly influenced by air temperature and canopy cover (AT, $P<0.01$; CON, $P<0.05$) (Fig. 2). ECM fungal species community composition was significantly correlated with soil temperature and canopy cover (ST, $P<0.05$; CON, $P<0.01$) (Fig. 2), but saprotrophic fungal species community composition had no significant relationship with the environmental variables tested. Canopy cover was significantly positively correlated with soil temperature, air humidity and air temperature ($P<0.05$, $R^2=0.120$; $P<0.05$, $R^2=0.022$; $P<0.05$, $R^2=0.067$).

NMDS indicated that total macrofungal and ECM fungal species community composition were significantly influenced by elevation, but saprotrophic fungal species community composition was not (Fig. 3). Multivariate analysis of variance confirmed that total macrofungal species community composition was significantly different between sites of 2,700–2,800 and 3,100–3,200 m.a.s.l., as well as between 3,100–3,200 and 3,300–3,400 m.a.s.l. ECM species community composition was significantly different between sites of 2,700–2,800 and 2,900–3,000 m.a.s.l.; 2,700–2,800 and 3,300–3,400 m.a.s.l.; and 2,900–3,000 and 3,300–3,400 m.a.s.l. ($P<0.01$). The relative abundance of ectomycorrhizal fungal genera was higher than that of saprotrophic fungal genera. The ratio of ECM fungi to saprotrophic fungi was approximately 3:1. The highest ratio was observed at around 2,900 m.a.s.l. and the lowest ratio was observed at 3,100 m.a.s.l. *Russula* was the dominant genus at all elevations, and the abundance of genera increased with elevation (Fig. 2). After *Russula*, *Lactarius* and *Suillus*, EMC fungi were the most dominant genera at all elevations.

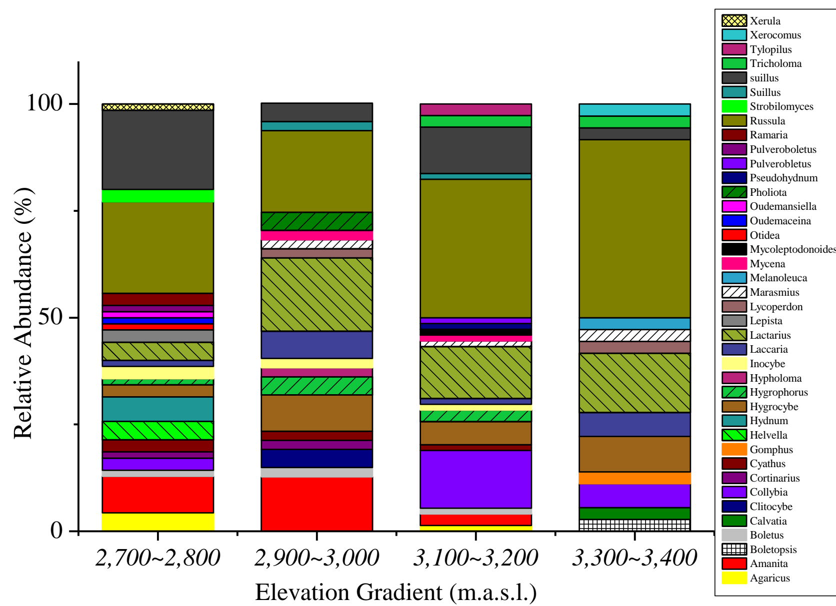

Fig. 2 Relative abundance of macrofungal genera collected from each of the plots along the elevation gradient used in the study, between June and October, 2014 on Yulong Snow Mountain, southwestern China.

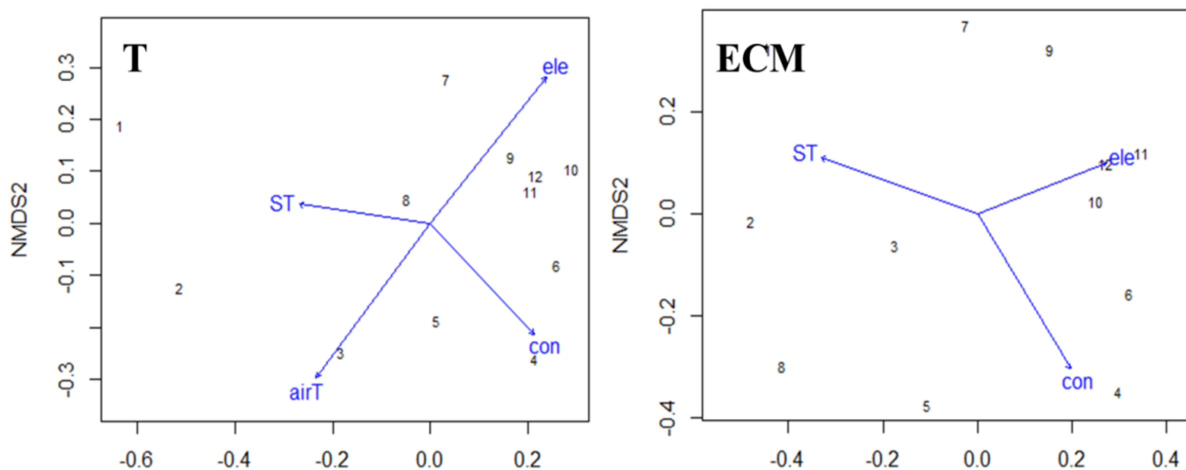

Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of the plots under environment factors based on macrofungal species communities. All of the displayed environment factors have passed a most significance test variables with argument p.max in R (p.max=0.1). T: total macrofungi; ECM: ectomycorrhizal fungi; ST: soil temperature; airT: air temperature; con: canopy cover; elevation.

Discussion

Our results indicate that soil temperature is the strongest predictor of total macrofungal and ECM fungal diversity, whereas air humidity has no significant effect on these groups. In contrast to these findings, Tedersoo et al (2014) reported that, on a global scale, mean annual precipitation was the strongest predictor of total macrofungal diversity. However, this does not necessarily hold true at a more local scale. Sporocarp strongly depends on environmental conditions such as temperature, air humidity, rainfall, and soil humidity (Lopez-Quintero et al. 2012, Kutszegi et al. 2015). According our results, species diversity is strongly correlated with air temperature, showing a

decline in diversity with a decline in temperature that are similar to those of Park et al. (2010) and Jang & Hur (2014). In addition to air temperature, both total macrofungal and ECM fungal species are positively correlated with soil temperature.

We observed lower macrofungal diversity on the higher slopes of the mountain, indicating that macrofungal species diversity is negatively correlated with elevation. This corroborates previous reports on declining diversity of species with increased altitude (Kernaghan & Harper 2001, Jang & Hur 2014). This is also confirmed by the work of Zhang et al. (2010), who reported a similar pattern in macrofungal diversity. The change in climatic conditions with increasing elevation has been suggested as a key contributing factor to this response (Bahram et al. 2012, Tello et al. 2015).

Canopy cover, which is positively correlated with soil temperature, air humidity and air temperature, had a positive influence on both total and ECM community composition. This finding is in agreement with the results of Santos-Silva et al. (2011). The increased shading associated with greater canopy cover reduced soil moisture loss, providing a suitable environment for macrofungal development (Gomez-Hernandez & Williams-Linera 2011). Furthermore, canopy cover is a strong predictor of total macrofungal and ECM fungal diversity. The relationship between vascular plants and macrofungal species richness and diversity was not analyzed because that is hard to find a significant relationship within a relatively small area (Chiarucci et al. 2005, Rudolf et al. 2013). Our results indicate that composition of the total macrofungal and ECM fungal communities are influenced by elevation. Temperature and humidity are directly linked to elevation and strongly affect the composition of macrofungal species communities via various mechanisms, including host species, enzymatic processes, soil moisture, and nutrient regimes (Villeneuve et al. 1989, Heinemeyer et al. 2004).

Our results indicate that the relative abundance and richness of ECM fungal genera are higher than that of saprotrophic fungi in subalpine pine forests, a conclusion which is supported by the findings of Geml et al. (2014). Our observation of positive correlations between the species abundance and richness of total fungi and ECM fungi highlights the dominance of ECM fungi over other soil fungal groups, and is in agreement with the work of Shi et al. (2014), who reported similar results for soil fungi in forests. We found no significant relationship between total fungi and saprotrophic fungi, again supported by the results of Shi et al. (2014). ECM fungi are known to suppress the presence of other soil fungi, further enhancing the dominance of ECM in these soils (Richard et al. 2004, Lindahl et al. 2010). Furthermore, ECM fungi and their host plants are tightly associated (van der Heijden et al. 2015). ECM fungi can boost plant growth and productivity and protect plant roots from heavy metal contamination, pathogens, diseases and stress (Baptista et al. 2010, Aucina et al. 2014), particularly in extreme environments (Li et al. 2014, Miyamoto et al. 2014). Low temperatures, strong UVB radiation, and dry soils are some of the extreme conditions which are characteristic of our plots (Ruotsalainen et al. 2009). The lower levels of saprotrophic fungal abundance compared to ECM fungal abundance in our study was probably due to the fact that leaf litter decomposes more slowly in subalpine pine forests, thus providing less substrate for the saprophytic fungi, as evidenced by the work of Rudolf et al. (2013).

Russula, an ECM genus, was dominant across all plots. Furthermore, the abundance of *Russula sp*. increased with elevation. Zhang (2014) found the same distribution pattern for *Russula* in the Laojun Mountains, a mountain range not far from our current sites; *Russula* is therefore likely to be the dominant fungal genus in the coniferous forests of subalpine forest. In addition, this indicates that the species diversity of *Russula* follows the opposite response to elevation in comparison with the other fungi surveyed in these forests.

The surveys of macrofungal species diversity during the rainy season were entirely based on monitoring sporocarp that can be visible to the naked eye. Below ground surveys of macrofungal communities using molecular techniques has become more frequent due to its' efficiently to identify all species present as compared to sporocarp in above-ground surveys. However, the sporocarp is more sensitive to environmental change than underground macrofungal mycelium (Tóth & Barta 2010). For example, sporocarp of most ectomycorrhizal species is more sensitive to additional nitrogen, full sun light and UV than mycelium (Mulder & de Zwart 2003). Sporocarp surveys can provide information about attributes of fungal communities and underlying functional processes of their ecosystems (Tóth & Barta 2010). Sporocarp surveys are also considered the primary basis for documenting fungal diversity (Richard et al. 2004).

Conclusion

Our study clearly shows that soil temperature and elevation strongly affect macrofungal diversity, richness, and community composition while air humidity has no impact in determining macrofungal community composition and richness in subalpine pine forest; our results also and highlight the dominance of ECM fungi over other macrofungi. Total macrofungal and ECM species diversity were significantly positively correlated with air temperature. Furthermore, total macrofungal and ECM fungal richness and diversity was significantly positively correlated with soil temperature, but negatively correlated with elevation. Community composition of total macrofungi and ECM fungi was significantly correlated with canopy cover and elevation gradients. The ratio of saprotrophic fungi to total macrofungi is lower than that of ECM fungi to total macrofungi, and has no significant relationship with total macrofungi in our study area. Diversity, richness, and community composition of saprotrophic fungi show no significant response to the environment variables studied. The information obtained can help better understand the effect of environment on macrofungi.

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