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Partial mutual exclusion of ectomycorrhizal and saprobic fungi in a tropical seasonal rainforest

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Abstract

Spatial distributions of ectomycorrhizal and saprotrophic fungi may differ in tropical forests for several reasons. If they do, it could have profound implications for carbon cycling across landscapes. We examined distributions of ectomycorrhizal and saprotrophic fungi in a 20 hectare forest study plot in China by collecting and identifying sporocarps (mushrooms) over two years. We found that for sporocarp numbers, species, and contributions to Shannon diversity, saprotrophic fungi were highest near stream channels and decreased with distance therefrom. Ectomycorrhizal species numbers and contributions to Shannon diversity were highest in plots most distant from stream channels. Earlier research here showed soil phosphorus availability to decrease away from stream channels, and ectomycorrhizal fungi should be favored where soil phosphorus is low. Aggressive negative interactions between these fungal guilds should intensify this pattern. We suggest that litter decomposition rates here should be highest near stream channels, because of strong domination by saprotrophic fungi.

Key words – ectomycorrhizal fungi – saprobic fungi – stream side ecology – tropical forests – Xishuangbanna

Introduction

Phosphorus (P) is the nutrient thought to most strongly limit plant growth in lowland tropical and subtropical forests (Vitousek 1984, Vitousek et al. 2010, Condit et al. 2013). Ectomycorrhizal (ECM) fungi were historically considered rare or absent from tropical ecosystems, but have been found in many forests (Corrales et al. 2018). Where detailed studies have been done, ECM associations were linked to low nutrient availability (Gartlan et al. 1986, Corrales et al. 2018).

Ectomycorrhizal fungi form symbioses with plant roots (Smith & Reed 2008) and extract phosphorus from large soil volumes and from soil chemicals not directly available to plant roots (Bolan 1991, Plassard & Dell 2010, Cairney 2011, Zhang et al. 2014). In return, they receive labile carbon directly from plant roots (Smith & Reed 2008). In contrast, saprobic (SAP) fungi live independently in soils and obtain their phosphorus and carbon solely by excretion of extracellular enzymes (Baldrian 2008). Some enzymes involved in extracellular digestion have been found in

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ECM fungi (Lindahl & Tunlid 2015), and ECM competes with decomposer microorganisms for access to organic N and P from the litter (Read & Perez-Moreno 2003).

In addition, these two fungal groups have negative interactions limiting their local co-existence (Singer & Araujo 1979, Lindahl 2000, Leake et al. 2001, McGuire et al. 2013, Marian et al. 2019). The ability of ECM fungi to perform slow saprobic decomposition of plant litter has been termed the "Gadgil Effect" (Fernandez & Kennedy 2016) and demonstrated in tropical forests (McGuire et al. 2010, Averill & Hawkes 2016). Both types disseminate spores via the production of fruiting bodies (mushrooms) that can be identified to species by traditional methods (Watling et al. 1995, Watling 2001, Henkel et al. 2011).

Besides soil properties affecting fungal communities, forest-floor litter is transferred downslope by overland water flow towards stream channels (Ghahramani et al. 2011, Bilby & Heffner 2016), potentially providing more resources for saprobic fungi in lower areas.

The tropical seasonal rainforest of Xishuangbanna is one of the most species-rich forest ecosystems in China (Cao & Zhang 1997). It is a biodiversity hotspot which contains over 5000 species of vascular plants, comprising 16% of the total plant diversity in China. It is therefore of great importance to global biodiversity conservation (Cao et al. 2008). Extensive research at Xishuangbanna Tropical Seasonal Rainforest Dynamics Plot (XTRDP) includes identification, location and mensuration of all tree stems (Lan et al. 2012) and spatially-explicit measurements of canopy litterfall and soil chemistry (Xia et al. 2015).

We hypothesized that ECM and SAP fungi have different spatial patterns across XTRDP, and collected and identified their mushrooms to examine that. We established replicated plots within 1 m of stream channels, those >1 and <160 m from stream channels, and those >160 m from stream channels. Those selections well-represent the entire Bubeng plot. We anticipated negative interactions between ECM and SAP fungi to differ across space, but previous research has examined this in low-disturbance tropical forests with high topographic variability.

Materials and Methods

Site selection and specimen collection

The site of this study was in Xishuangbanna, China at 21º08' and 22º36' N, 99º56' and 101º50' E. Xishuangbanna covers an area of 19120 km^2 that has mountainous topography and a typical monsoon climate (Cao et al. 2008). The annual mean temperature is 21.8 ºC, and annual mean precipitation is 1493 mm, of which about 85% occurs in the rainy season between May to October. The dry season lasts from November to April (Cao et al. 2008).

The 20-ha XTRDP (Fig. 1) was established in a *Parashorea chinensis* forest within Mengla County, Xishuangbanna Prefecture, Yunnan Province, south western China. Mengla borders with Lao People's Democratic Republic. The XTRDP covers 101º34' 26" ~ 101º34' 47" E, 21º36' 42" ~ 21º36' 58" N and its canopy height is 40 to 60, with three tree layers plus a shrub and herbaceous layer. The XTRDP is rectangular and measures 400 m (north-south) by 500 m (east-west). The elevation of the plot ranges from 709 to 869 m above sea level, with the highest elevation in the northwest of the plot (Fig. 1).

The upper canopy is dominated by *Parashorea chinensis*, *Salonea tomentosa* (Benth.) Rehder & E.H. Wilson, *Pometia tomentosa* (Blume) Teijsm. & Binn., *Semecarpus reticulate* Lecomte, and *Barringtonia pendula* Kurz. The lower canopy mainly consists of *Garcinia cowa* Roxb, *Knema furfuracea* (Hook. F. & Thomson) Warb, *Nephelium chryseum* Blume, *Cinnamomum bejolghota* (Buch.-Ham.) Sweet, *Baccaurea ramiflora* Lour., *Pittosporopsis kerrii* Craib., *Mezzettiopsis creaghii* Ridl., *Saprosma ternate* Hook. F, and *Leea compactiflora* Kurz (Cao et al. 2008).

Three perennial streams run through this 20-ha plot and converge near the southeastern corner. The distance between their entry to the plot and their point of convergence is 800 m, 500 m, and 450 m and have average widths of 8, 6 and 6.5 m respectively. These streams are shaded by the canopies of the tree species *Garcinia cowa*, *Cinnamomum bejolghota*, *Knema furfuracea* (Hook. F. & Thomson) and *Diospyros hasseltii* Zoll. Various species of macrofungi grow on both sides of

these streams and at higher elevations, with their distribution and growth being determined by environmental factors, including light, moisture, temperature and essential nutrients.

For this study, 400 m^2 area of each site (site A is within 1 m of streams, site B was 1 to 160 m away and site C was further than 160 m from the stream) was selected from each creek with 6 replicates from each site. We selected 400 m^2 areas from both sides (left and right facing upstream) of three streams (Fig. 1). The 400 m^2 area consisted of 400 plots of 1m ×1m where the minimum distance between two plots was 1m and the maximum distance between two plots was 3 m. Macrofungal sporocarps were collected from July to October in 2014 and 2015 into individual polyethylene bags.

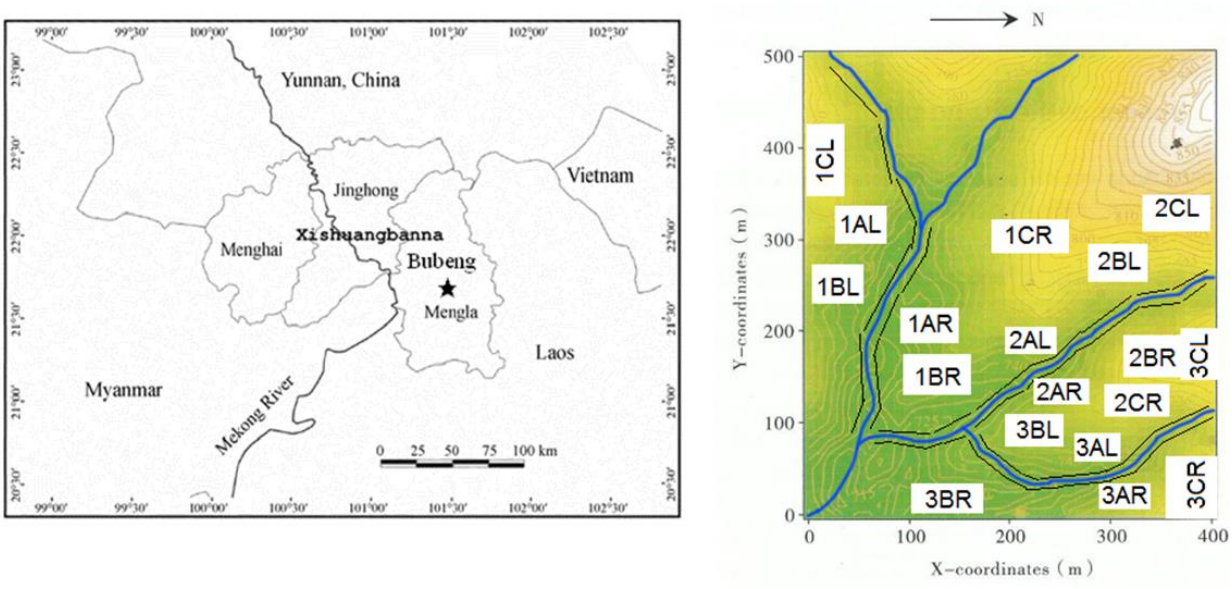

Fig. 1 – Left panel. Location of the 20-hectare tropical seasonal rainforest dynamics plot in Xishuangbanna, southwest China. Right panel. Elevation map of the 20-hectare plot with 5 m contours. Approximate locations of sampling sites and plots are also shown. See text for additional details.

Identification of sporocarps

All specimens of macrofungi were examined in the laboratory. Records were made of apparent macromorphological characteristics such as colour, shape and size of the macrofungi cap, stipe, gills and other characteristics such as odour, colour changes and habitat. Spore prints were made to determine the colour of the basidiospores and were then used for basidiospore measurements. Microscopic examinations were performed using Nikon Model Eclipse Ci-s research microscopes. Characteristics of macrofungi, colour of spore print, microscopic analysis, books, monographs (Corner 1966, Guzmán 1983, 1968, Phillips 1981, Moser 1983, Arora 1986) and journal articles (Das et al. 2013, Itoo et al. 2013, Lodge & Overbo 2008, He et al. 2010) were used to identify most of the macrofungi specimens to species level. The taxonomic classification of species was based on Kirk et al. (2008), and Index Fungorum (2017) was followed for the nomenclature. After examination, specimens were dried in a portable food dryer for 24–32 hours at 35ºC and were sealed separately in polyethylene bags.

Data analysis

To calculate diversity of macrofungi in different sites, Shannon's diversity index (shown below) was used, where H = the Shannon diversity index; Pi = fraction of the entire population made up of species; S = numbers of species encountered; ∑ = sum from species 1 to species S.

$$H = -\sum_{j=1}^{S} p_i \ln p_i$$

Each of those species collected contributes to Shannon diversity. The contribution to Shannon Diversity index for all SAP and ECM fungi was calculated.

Results

Across 3600 m^2 of Bubeng plot sampled during peak emergence periods over two years, 25678 SAP and 9946 ECM sporocarps were collected and identified to species. They included 66 SAP and 38 ECM species. Their distributions were strikingly non uniform and in many cases were related to distances from stream channels. The general pattern was the domination of saprobes along the stream sides, while high ECM species richness and diversity increased further away from streams. Support for and exceptions to this pattern are described below.

Three of the 4 most abundant SAP fungi species were uniformly distributed across sampling sites (*Microporus xanthopus*, *Trametes versicolor* and *Pleurotus ostreatus*) (Table 1). Other saprobes more abundant than any Basidiomycete ECM species had 4 of 5 species limited to streamside sites; *Microporus affinis*, *Polyporus squamosus*, *Polyporus badius* and *Polyporus brumalis* (Table 1). At lower species abundances down to 172 individuals identified, 22 of 32 SAP species were limited to streamside sites (Table 1). Ascomycete SAP species were completely restricted to streamside sites (Table 1).

The most abundant Ascomycete ECM species was found in all 3 sites (*Xylaria cubensis*, Table 2), but Ascomycete *Xylaria longipes* was restricted to stream sides, opposing general pattern seen here. The three Basidiomycete ECM species in terms of abundance (*Laccaria laccata*, *Lactarius sanguifluus* and *Russula maculata*) also did not support general patterns seen here, being either found across sites or restricted to stream sides (Table 2). At lower species abundances down to 88 individuals identified, 17 of 19 ECM species were absent from streamside sites, and generally more abundant in plots of site C furthest from stream channels (Table 2).

Streamside site A plots averaged 2804 individuals of 39 saprobic species and 760 individuals of 9 ECM species (Tables 1, 2), with 80% of Shannon diversity from saprobic species (Fig. 2). Site B plots more distant from streams averaged 1067 individuals of 20 saprobic species and 329 individuals of 15 ECM species (Tables 1, 2), with 72% of Shannon diversity from saprobic species (Fig. 2). Site C plots furthest from streams averaged 409 individuals of 15 saprobic species and 569 individuals of 26 ECM species (Tables 1, 2), with only 44% of Shannon diversity from saprobic species (Fig. 2).

Of 66 SAP species, 39 were restricted to streamside site A plots, while only 8 were found in all 3 sites (Table 1). Only 16 saprobic species were absent from Site A. Of 38 ECM species, 28 were absent from streamside site A plots, while only 2 were found in all 3 sites (Table 2).

In summary, the most abundant SAP and ECM species were either ubiquitous or their distributions opposed this overall spatial patterning. Those species did not appear sensitive to aggressive effects of the other feeding type, or to soil chemical or other spatial patterns. Mutual partial exclusion of fungal feeding types arose from species of intermediate abundance.

Discussion

Down slope transfer of forest-floor litter has been demonstrated elsewhere (Ghahramani et al. 2011, Bilby & Heffner 2016), and would provide additional resources for SAP fungi near to stream channels. However, leaf and wood litter are abundant in all areas of this forest, so saprotrophic limitations far from stream channels does not seem likely. ECM dominance of fungal communities most distant from streams cannot be ascribed to soils being always wet near streams, because densities of ECM sporocarps were highest in streamside plots. Rather it is that SAP

species, numbers and diversity fall with distances from stream. Meanwhile, ECM species richness and diversities increased further from the stream channels.

A more probable explanation can be drawn from Xia et al. (2015), who found that the available phosphorus in the forest soil was highest near stream channels. It decreased approximately four-fold in areas most distant from stream channels that they measured. Other research shows that ECM are favored in areas of low soil nutrient availability, including that of phosphorus (e.g. Read & Perez-Moreno 2003, Corrales et al. 2018).

Table 1 Saprotrophic sporocarps collected from Bubeng Tropical Seasonal Rainforest Dynamics Plot (XTRDP) at Xishuangbanna, China. Orders in bold are Ascomycetes and others Basidiomycetes. Species are listed in decreasing order of total sporocarp numbers collected. Sites A, B and C refer to distances from stream channels (see text). In each site, six plots were sampled and means and (standard deviations) are presented. Blanks indicate species were absent from sites. Values in bold red indicate species whose distributions particularly support community pattern of saprotrophs.

Order	Species name (saprotrophic)	Total sporocarps	Site A plot means (std dev)	Site B plot means (std dev)	Site C plot means (std dev)
Polyporales	*Microporus xanthopus*	3737	253 (125)	261 (79)	109 (22)
Polyporales	*Trametes versicolor*	3234	271 (41)	202 (5)	66 (30)
Xylariales	*Xylaria cubensis*	3148	292 (45)	158 (17)	75 (13)
Polyporales	*Microporus affinis*	1594	**266 (106)**		
Xylariales	*Xylaria longipes*	1170	195 (148)		
Agaricales	*Pleurotus ostreatus*	1223	80 (36)	81 (3)	44 (17)
Polyporales	*Polyporus squamosus*	1094	**182 129)**		
Polyporales	*Polyporus badius*	906	**151 (107)**		
Polyporales	*Ganoderma lucidum*	871	2 (5)	143 (25)	
Polyporales	*Polyporus brumalis*	847	**141 (94)**		
Agaricales	*Crucibulum leave*	625	41 (34)	29 (19)	35 (2)
Pezizales	*Cookeina tricholoma*	628	**105 (74)**		
Polyporales	*Polyporus leptocephalus*	580	**97 (63)**		
Pezizales	*Cookeina venezuelae*	530	**88 (62)**		
Polyporales	*Ceriporiopsis merulinus*	476	**79 (99)**		
Agaricales	*Marasmius oreades*	462		50 (15)	27 (8)
Geastrales	*Geastrum fimbriatum*	455	**76 (6)**		
Agaricales	*Marasmiellus ramealis*	432	**72 (14)**		
Geastrales	*Geastrum triplex*	407		35 (12)	33 (3)
Agaricales	*Lentinula edodes*	404		67 (27)	
Auriculariales	*Auricularia auricula-judae*	400	**67 (10)**		
Agaricales	*Panellus stipticus*	351	59 (34)		
Agaricales	*Lepiota helveola*	349		38 (23)	20 (6)
Polyporales	*Daedalea sp*	307	**51 (20)**		
Agaricales	*Mycena leaiana*	306	21 (13)	18 (4)	13 (2)

Table 1 Continued.

Order	*Species name* (saprotrophic)	Total sporocarps	Site A plot means (std dev)	Site B plot means (std dev)	Site C plot means (std dev)
Agaricales	*Stropharia ambigua*	299	18 (12)	17 (2)	15 (2)
Auriculariales	*Auricularia delicate*	296	46 (20)	4 (9)	
Agaricales	*Marasmius rotula*	265	44 (28)		
Agaricales	*Pleurotus citrinopileatus*	260	43 (25)		
Agaricales	*Marasmius bulliardii*	256	43 (34)		
Polyporales	*Neofavolus alveolaris*	255	43 41)		
Geastrales	*Geastrum floriforme*	248	41 (38)		
Geastrales	*Geastrum saccartum*	247	41 (31)		
Pezizales	*Phillipsia domingensis*	247	41 (29)		
Polyporales	*Nigroporus durus*	244	41 (22)		
Agaricales	*Marasmius siccus*	232	39 (28)		
Agaricales	*Marasmius epiphyllus*	231	39 (36)		
Pezizales	*Phillipsia hartmannii*	208	35 (32)		
Agaricales	*Pleurotus eryngii*	197		33 (12)	
Agaricales	*Collybia cookei*	183	31 (10)		
Auriculariales	*Auricularia polytricha*	183		31 (2)	
Agaricales	*Collybia dryophila*	172	29 (9)		
Agaricales	*Hymenopellis radicata*	165	28 (12)		
Agaricales	*Micropsalliota globocystis*	157		13 (2)	14 (5)
Agaricales	*Collybia umbonata*	148	25 (8)		
Agaricales	*Mycena galopus*	144	24(4)		
Hymenochaetales	*Phellinus gilvus*	144	24 (37)		
Agaricales	*Psathyrella hydrophila*	121		11 (1)	9 (3)
Polyporales	*Tyromyces chioneus*	85		3 (2)	12 (3)
Agaricales	*Agaricus campestris*	81	2 (5)	5 (1)	6 (4)
Polyporales	*Trametes trogii*	68	6 (15)	3 (8)	2 (5)
Agaricales	*Xerula radicata*	55		7 (3)	2 (4)
Agaricales	*Hypsizygus tessellatus*	44		7 (8)	
Agaricales	*Agaricus bisporus*	31	5 (13)		
Agaricales	*Pleurotus pulmonarius*	26	4 (11)		
Agaricales	*Entoloma strictius*	25	2 (6)	2 (4)	
Agaricales	*Marasmius sullivantii*	24	4 (10)		
Agaricales	*Crepidotus mollis*	21		4 (9)	
Agaricales	*Pleurotus australis*	14		2 (6)	
Agaricales	*Crepidotus crocophyllus*	13	2 (5)		

Table 1 Continued.

Order	*Species name* (saprotrophic)	Total sporocarps	Site A plot means (std dev)	Site B plot means (std dev)	Site C plot means (std dev)
Polyporales	*Microporus badius*	13		2 (5)	
Agaricales	*Clitocybe phyllophila*	11	2 (4)		
Agaricales	*Crucibulum serratum*	11			2 (4)
Polyporales	*Ganoderma zonatum*	11	2 (4)		
Agaricales	*Entoloma rugosum*	10		2 (4)	
Agaricales	*Entoloma lampropus*	6	1 (2)		
Polyporales	*Ganoderma multipileum*	5	1 (2)		
Agaricales	*Entoloma luteum*	4	1 (2)		

Three of the 4 most abundant SAP species were uniformly distributed across sampling sites (*Microporus xanthopus*, *Trametes versicolor* and *Pleurotus ostreatus*) (Table 1). Other saprobes more abundant than any Basidiomycete ECM species had 4 of 5 species limited to streamside sites; *Microporus affinis*, *Polyporus squamosus*, *Polyporus badius* and *Polyporus brumalis* (Table 1). At lower species abundances down to 172 individuals identified, 22 of 32 SAP species were limited to streamside sites (Table 1). Ascomycete SAP species were completely restricted to streamside sites (Table 1).

Table 2 Ectomycorrhizal sporocarps collected from Bubeng Tropical Seasonal Rainforest Dynamics Plot (XTRDP) at Xishuangbanna, China. Orders in bold are Ascomycetes and others Basidiomycetes. Species are listed in decreasing order of total sporocarp numbers collected. Sites A, B and C refer to distances from stream channels (see text). In each site, six plots were sampled and means and (standard deviations) are presented. Blanks indicate species were absent from sites. Values in bold red indicate species whose distributions particularly support community pattern of ectomycorrhizae being more dominant away from stream channels (see text).

Order	*Species name* (Eectomycorrhizal)	Total sporocarps	Site A plot means (std dev)	Site B plot means (std dev)	Site C plot means (std dev)
Agaricales	*Laccaria laccata*	658	44 (51)	30 (5)	35 (3)
Russulales	*Lactarius sanguifluus*	625	104 (102)		
Russulales	*Russula maculata*	444	52 (64)		22 (3)
Boletales	*Xerocomus communis*	317		**23 (3)**	**75 (13)**
Boletales	*Boletus edulis*	230		**16 (2)**	**22 (2)**
Boletales	*Suillus luteus*	223			**37 (2)**
Boletales	*Tylopilus violatinctus*	197		**13 (1)**	**20 (2)**
Boletales	*Boletus bicolor*	193		**16 (7)**	**17 (3)**
Boletales	*Strobilomyces polypyramis*	192		**9 (2)**	**23 (3)**
Cantharellales	*Cantharellus cibarius*	192		**13 (1)**	**20 (3)**

Table 2 Continued.

Order	*Species name* (Eectomycorrhizal)	Total sporocarps	Site A plot means (std dev)	Site B plot means (std dev)	Site C plot means (std dev)
Boletales	*Suillus granulates*	191			**32 (13)**
Russulales	*Lentinus crinitus*	187	31 (26)		
Agaricales	*Cortinarius orellanosus*	186	31 (8)		
Boletales	*Xerocomus subtomentosus*	172			**29 (3)**
Boletales	*Xerocomus truncates*	147			**25 (4)**
Agaricales	*Amanita vaginata*	140		**1 (2)**	**23 (2)**
Russulales	*Lactarius pyrogalus*	125			**21 (1)**
Boletales	*Boletus speciosus*	123		21 (9)	
Agaricales	*Amanita virosa*	118		6 (4)	13 (4)
Boletales	*Phlebopus portentosus*	113		7 (1)	12 (2)
Russulales	*Russula emetica*	99			17 (2)
Russulales	*Lactarius piperatus*	88			15 (4)
Agaricales	*Amanita flavorubescens*	83	2 (2)	1 (1)	11 (5)
Agaricales	*Laccaria bicolor*	76			13 (3)
Agaricales	*Laccaria proxima*	75			13 (2)
Agaricales	*Cortinarius flexipes*	74			12 (6)
Boletales	*Boletellus emodensis*	69			12 (2)
Thelephorales	*Thelephora ganbajun*	69		12 (4)	
Agaricales	*Cortinarius fulviconicus*	56			9 (2)
Agaricales	*Amanita rubrovolvata*	53			9 (2)
Boletales	*Scleroderma citrinum*	39	7 (4)		
Boletales	*Strobilomyces strobilaceus*	33		2 (5)	4 (9)
Boletales	*Boletus badius*	16		3 (7)	
Agaricales	*Inocybe rimosa*	11	2 (4)		
Thelephorales	*Thelephora terrestris*	10		2 (4)	
Agaricales	*Inocybe geophylla*	4			1 (2)

Edaphic patterns influence fungal distributions in XTRDP. Widely reported aggressive interactions between ECM and SAP (e.g. Leake et al. 2001, McGuire et al. 2013, Marian et al. 2019) would intensify community differences across space. However, it must be noted that the most abundant ECM and SAP species were indifferent to such patterns. Instead, community differences arose from patterns of species of intermediate abundance. We are not aware of previous research showing this.

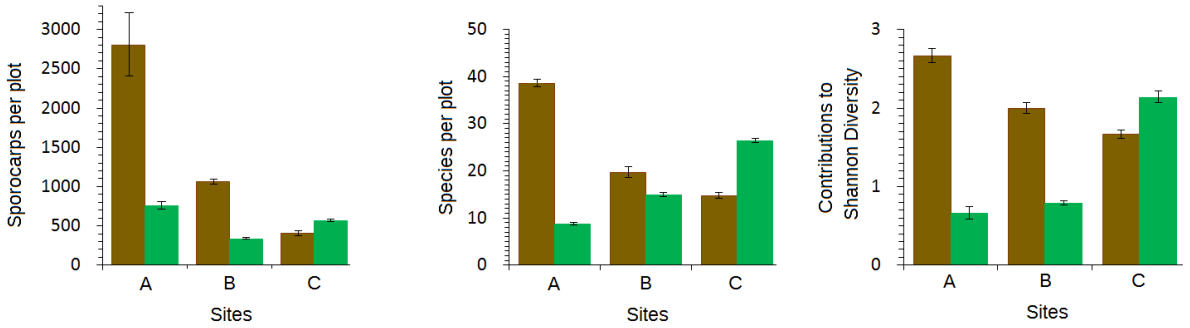

Fig. 2 – Distributional patterns of saprotrophic (brown) and ectomycorrhizal (green) macrofungal sporocarps collected from Bubeng Tropical Seasonal Rainforest Dynamics Plot at Xishuangbanna, China. Site A is within 1 meter of stream channels, site B is >1 meter and <160 meters from stream channels, site C is >160 meters from stream channels. Each site has 6 plots totaling 1200 m2 sampled area. Sporocarps per plot, species per plot and contributions to Shannon diversity are shown separately. Statistical dispersions are standard deviations over 6 plots. See text for additional details.

In the Korup Forest Dynamics Plot in Cameroon, ECM distributions varied across space (Bechem et al. 2014) but were not related to soil-phosphorus distributions (Gartlan et al. 1986). This distinction may relate to the fact that tree species hosting ECM in tropical Africa mostly host nitrogen-fixing bacteria as well (Bâ et al. 2012); a pattern absent from Asian tropical forests. So, soil-nutrient availability may not always be the driving force for macrofungal distributions in tropical forests.

Studies assessing ECM based on identifiable sporocarps above the litter layer might miss underground sporocarps. Our sampling over two years covered the entire period of sporocarp emergence for both ECM and SAP in this forest, so incomplete sampling is unlikely.

Effects from limitations from soil chemistry or interactions on this fungal community were incomplete, as the most abundant saprobic and ectomycorrhizal species did not respond to them. However, the rest of the fungal community did, and created patterns were observed in the current study. In this tropical forest, some aspects of the Gadgil effect (negative interactions between ECM and SAP structuring fungal communities; Gadgil & Gadgil 1971, Lindahl 2000, Leake et al. 2003) have been demonstrated. This raises questions as to whether plant-litter or soil organic matter decomposition rates vary spatially in XTRDP, similar to other studies which have shown fungal community differences (Cairney & Meharg 2002, Averill & Hawkes 2016, Fernandez & Kennedy 2016, Corrales et al. 2018). That would be a complete local demonstration of the Gadgil effect and could be examined by leaf litter and buried soil (organic matter) decomposition studies across the XTRDP, using appropriately sized mesh bags. Those could have implications for carbon cycling in other tropical forests, where soil-phosphorus levels also vary and may alter fungal community structure and function. Fungal spatial patterns shown here may be seen both as an example of, and a tool available for exploration of tropical carbon cycling.

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