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The importance of plot size and the number of sampling seasons on capturing macrofungal species richness

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ABSTRACT

The species-area relationship is an important factor in the study of species diversity, conservation biology, and landscape ecology. A deeper understanding of this relationship is necessary, in order to provide recommendations on how to improve the quality of data collection on macrofungal diversity in different land use systems in future studies, a systematic assessment of methodological parameters, in particular optimal plot sizes. The species-area relationship of macrofungi in tropical and temperate climatic zones and four different land use systems were investigated by determining the macrofungal species richness in plot sizes ranging from 100 m^2 to 10 000 m^2 over two sampling seasons. We found that the effect of plot size on recorded species richness significantly differed between land use systems with the exception of monoculture systems. For both climate zones, land use system needs to be considered when determining optimal plot size. Using an optimal plot size was more important than temporal replication (over two sampling seasons) in accurately recording species richness.

1. Introduction

Fungi play a key role in ecosystem function due to their contribution to the distribution of nutrients and energy flow within their environment. In addition to their ecological functions, macrofungi, which form aboveground and belowground fruiting bodies (Redhead, 1997), are of economic importance and provide alternative income sources for rural communities worldwide (He et al., 2011; Lee et al., 2009; Mortimer et al., 2012). There have been many studies of the ecological functions (Balaes et al., 2017; Courty et al., 2010; Priyamvada et al., 2017; Rayner and Boddy, 1988; van der Heijden et al., 1998) and economic potential (Dai et al., 2009; Lee et al., 2009; McLellan and Brown, 2017; Yilmaz and Zencirci, 2016) of macrofungi, across a range of environments. To understand the ecological and economic role of macrofungi in specific environments, it is crucial to capture a representative sample of the richness and abundance of the macrofungal community (O'Hanlon and Harrington, 2012b; Smith et al., 2002). However, many previous studies have lacked any strategic optimization of sampling design and methodologies, making it difficult to evaluate and compare their findings.

A major factor influencing the estimates of population size is the distribution pattern of the studied organisms. Population distribution patterns describe the spatial and temporal occurrence of an individual of the population in its habitat (Li et al., 2000). The heterogeneous distribution of macrofungi communities poses challenges to population estimates (Palmer and White, 1994). Macrofungal distribution is driven by soil properties (Reverchon et al., 2012; Tedersoo et al., 2011), microclimatic conditions (Brown et al., 2006), and potential interactions of fungi with vegetation (Bonet et al., 2004; Burke et al., 2009; Gao et al., 2015). Distribution patterns are further complicated by the anatomy of a typical fungal body that consists of a large belowground mycelial network which results in a clustering of fruiting bodies within the

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landscape (Fukiharu and Kato, 1997; Kikuchi and Futai, 2003; Miyamoto and Igarashi, 2004). Previous studies have used a wide range of scales to investigate the spatial distribution and diversity of macrofungal fruiting body in specific forest types. For example, Henkel et al. (2012) established 10 000 m^2 plots that were further subdivided into 100 m^2 subplots to survey macrofungal diversity in *Dicymbe*-dominated forests. O'Hanlon and Harrington (2012a) set up 100 m^2 plots to survey macrofungal diversity in Atlantic oak forests. Miyamoto and Igarashi (2004) studied *Collybia pinastris* in 30 m^2 plots that were divided into subplots of 0.5 m × 0.5 m. Kikuchi and Futai (2003) investigated the fine scale distribution of *Suillus pictus* using 72 m^2 plots, subdivided into 1 m × 1 m subplots. As the formation of fruiting bodies depends on favorable environmental conditions (Gassibe et al., 2015), macrofungal diversity and abundance exhibits a distinct seasonality (Luoma et al., 1991). Therefore, sampling design, especially regarding sufficient plot size and coverage of several seasons, is likely to strongly affect the outcomes of studies investigating macrofungal fruiting bodies. To provide recommendations on how to improve the quality of future studies on macrofungal diversity in different land use systems, a systematic assessment of methodological parameters, especially regarding optimal plot sizes, is required.

The relationship between increases in the size of a sampled area and increase in the number of species that reside in that area is non-linear (Schoener, 1976). This 'species-area relationship' has been of interest in ecology for more than a century (Jaccard, 1912) and is important for the study of species diversity, conservation biology, and landscape ecology (Lomolino, 1989, 2000; Palmer and White, 1994). Within a given land use system, plotting the sampled area against the number of species, for a series of samples from increasing plot sizes, characteristically produces a monotonically increasing curve with a sharp slope at the beginning that then reaches a plateau. De Candolle (1855) and Jaccard (1902, 1908) reported patterns, that were subsequently formalized as the species-area curve (Arrhenius, 1921; Cain, 1938; Gleason, 1922). Many studies have shown that macrofungal diversity differed between forest types (Brown et al., 2006; Gates et al., 2011; O'Hanlon and Harrington, 2012a; Ortega and Lorite, 2007). Therein, Brown et al. (2006) showed that habitat requirements determined macrofungal distribution at a landscape scale. Although the overall species-area pattern among plants, animals or fungi may be similar, there is little research on the relationship between species richness of macrofungi and sampling area in different land use systems. Previous studies have indicated that climatic factors affect macrofungal formation (Gassibe et al., 2015; Luoma et al., 1991; O'Dell et al., 2000), however research on the impact of climatic zones on the relationship between species richness and sampling area is lacking. Much macrofungal research has come from temperate and tropical areas (Henkel et al., 2012; Lindblad, 2000; Yamashita et al., 2009; Zhang et al., 2010). To obtain results comparable with these previous studies, two climate types and four land use systems were selected for this study.

In our study, we aim to i) evaluate the importance of different sampling designs and size of sampling plots to capture species richness of macrofungi, ii) assess the relationship between plot size and prediction of the most abundant genera in a larger landscape, and iii) test the relative importance of plot size and repeated sampling seasons, in capturing maximum species richness. We investigated the species-area relationship of macrofungi in two different climatic zones (temperate and tropical) and four different land use systems (mixed forest, pine monoculture, tree-based agriculture, and grassland) by determining the macrofungal species richness in plot sizes ranging from 100 m^2 to 10 000 m^2 and including two sampling seasons.

2. Materials and methods

2.1. Study areas

This study was carried out in six study sites, five of which were in China and one in Thailand. The geographic range of these sites spans 800 km from northwest Yunnan to southwest Yunnan to northern Thailand (Fig. SI1). Four land use systems (mixed forests, pine monoculture, tree-based agriculture, and grassland) were selected within the six sites. Tree-based agriculture refers to agricultural systems that have trees incorporated into them, for example, tea plantations using tea trees, rubber plantations with a coffee understory. Site 1 (Zhong Dian - ZD) with two land use systems, and site 2 (Lijiang - LJ) with one land use system are in northern Yunnan and have a temperate climate. Site 3 (Baoshan - BS) with three land use systems is in western Yunnan, and has a temperate climate. Site 4 (Mengsong - MS) with two land use systems is in the uplands of tropical southern Yunnan. Only one dominant land use system was selected within Site 5 (Mengla - ML), which is in the lowlands of tropical southern Yunnan. Two land use systems were selected at site 6 (Doi Mae Salong - DMS), which is in tropical northern Thailand. Detailed site information regarding location, elevation, and climate are provided in Table 1, including the mean monthly temperature and rainfall during the rainy season (May to October) from 2012 to 2014. Data on dominant tree species and land use systems for each site are given in Table 2. Meteorological data (rainfall and temperature) were obtained from two sources: the China Meteorological Data Service Center (http://cdc.nmic.cn/home.do), and the Upper Northern Region Irrigation Hydrology Center (http://hydro-1.net/home.php) for Thailand.

2.2. Plot design

Within each land use system we randomly placed 100 × 100 m large sampling areas. Within this largest sampling area of 10 000 m^2 (100 × 100 m), a 400 m^2 (20 × 20 m) plot was placed in the center (other 400 m^2 plots were set up outside the 10 000 m^2 plot) and along the diagonal axis three 100 m^2 plots (10 × 10 m) were established (Fig. SI2). This plot combination was set up in each land use system present at each site. Depending on the availability of local land use systems in each location, the plot combination was replicated in same land use system up to three times, details on the number of plot replicates in each location are listed in Table 1. GPS points were used to mark the margin of 10 000 m^2 plots, while the 400 m^2 and 100 m^2 plots were measured by tape measure and compass to avoid GPS inaccuracies at fine scales. A vegetation survey was carried out in 2013, dominant tree species in the 10 000 m^2 plots were identified. All plot designs at different sites are shown in Fig. SI2 and Table 1.

2.3. Macrofungal fruiting body sampling and identification

Macrofungal sampling was carried out weekly during the rainy season (May–September) in 2013 and 2014. All fruiting bodies with a cap diameter of >1 cm were sampled, photographed, and their information recorded (habitat, plot name, forest type, collecting date) (Bonet et al., 2012). Solitary, scattered or grouped fruiting bodies of the same species within a given grid cell were all recorded as a single observation (Brown et al., 2006). All fresh fruiting bodies were brought to the laboratory for macro- and micromorphological analysis. Collections were dried using an electric fruit dryer (40 °C) and stored in sealed plastic bags at room temperature. The collections were deposited in the Herbarium of Kunming Institute of Botany (HKAS), Chinese Academy of Sciences, China.

Fruiting bodies were identified in the laboratory. Eighty-nine percent of macrofungi were identified to species level, with the remainder identified to genus level by using macro- and micro-morphological features with applicable keys, mushroom color guides and monographs (Liang, 2007; Peng et al., 1992; Wu et al., 2010; Yang, 2005; Zhao and Zhang, 2000; Zhou et al., 2006). The taxonomic classification of species was based on Kirk et al. (2008), and the nomenclature follows Index Fungorum (2018).

2.4. Data analysis

In this study, species richness was assessed according to Baptista et al. (2010) and refers to the number of species taxa of macrofungal fruiting bodies collected from each plot. To analyze the effect of increasing plot size on species richness we compared the species richness of the macrofungi in the two smaller plots (100 m^2, 400 m^2) against that found within the 10 000 m^2 plot. Based on the maximum species richness in the largest plots (10 000 m^2) we then calculated the mean relative percentage of species richness covered in smaller plot areas (100 m^2, 400 m^2). The mean relative percentage of species richness was calculated using the mean ratio of species richness captured in 100 m^2 and 400 m^2 against that in the 10 000 m^2 plots. We calculated the relative percentage species richness captured in the 100 m^2 and 400 m^2 subplots against in each of the 10 000 m^2 plots in which these subplots were located; then the mean percentage species richness in the same land use system for the 100 m^2 and 400 m^2 subplots was calculated. For this purpose, we grouped the sampled plots according to land use systems and climatic zones. We also ranked different land use systems and climate types according to their absolute species richness for all sampled plot sizes (100 m^2, 400 m^2, and 10 000 m^2). Only data collected from 10 000 m^2 plots that had 100 m^2 and 400 m^2 subplots within them were considered for this analysis (i.e. 2014 data).

To evaluate the effect of sampling season on macrofungal species richness, for each plot we compared the macrofungal species richness of a given area during one season with the species richness recorded during two sampling seasons. This data analysis utilized all data from the 100 m^2 and 10 000 m^2 plots, from 2013 to 2014. We determined the most abundant genera from our data set of each land use system and plot size. This was determined by calculating the highest percentage occurrence of a given genus in each plot (genus % = the number of individuals from a genus/the total number of individuals from all genera × 100). For this data analysis only those 10 000 m^2 plots that had 100 m^2 and 400 m^2 subplots within were considered (Table 1). We assumed that the most abundant genus found in each 10 000 m^2 plot provides an adequate representation of its true abundance across each land use system, we then calculated how closely results from the smaller subplots corresponded to results from the 10 000 m^2 plots. For each plot level we calculated the percentage of subplots in which we recorded the same most abundant genera as in the corresponding 10 000 m^2 plots. Macrofungal species richness in the three single 100 m^2 plots (total area is 300 m^2), located inside the 10 000 m^2 plots, was also calculated to obtain a wider range of comparative plot sizes. The effect of climatic zones and land use systems was analyzed using one-way ANOVA and Mann-Whitney rank sum test. This data analysis only utilized the 10 000 m^2 plots that had 100 m^2 and 400 m^2 subplots within them. Initial calculations were carried out in Office Excel 2010. Graphs and statistical analyses used Sigmaplot version 12.5 (Systat, California, USA). A level of $p \leq 0.05$ was used as the threshold for significance.

3. Results and discussion

3.1. Effect of plot size on captured macrofungal species richness

Absolute species richness is central to the description and evaluation of macrofungal populations across different land use systems (Baptista et al., 2010; Smith et al., 2002). To determine whether the size of the plot affected estimates of species richness, we compared the changes of absolute species richness with increasing sampling area for different land use systems. In monoculture systems in temperate land use systems (grassland and

Table 1
Number of plots and subplots sampled in each study area and detailed site information. Numbers in brackets give the number of 400 m^2 plots located in the same land use system, but outside the 10 000 m^2. Land use systems are abbreviated as CF: Conifer forest, MF: Mixed forest, GL: Grassland, PMF: Mixed forest dominated by pine, QMF: Mixed forest dominated by *Quercus* species, RDF: Mixed forest dominated by *Rhododendron* species, PF: Pine forest, OMF: Old mixed forest, MS-SMF: Secondary mixed forest, TP: Tea plantation, CR: Coffee and rubber plantation, BMF: Mixed forest dominated by bamboo, RMF: Regrowth mixed forest. MR: Mean rainfall during the rainy season (May to October) from 2012 to 2014, MT: Mean temperature during the rainy season (May to October) from 2012 to 2014.

Site name	Climatic region	Plot description	No. of 10 000 m^2 plots	No. of 400 m^2 plots	No. of 100 m^2 plots	Longitude	Latitude	Elevation (masl)	MR (mm)	MT (°C)
Zhongdian (ZD)	Temperate	ZD-CF	2	5 (3)	3	99°51′19″	27°29′10″	3260	82.4	12.3
Zhongdian (ZD)	Temperate	ZD-MF	3	5 (2)	6					
Zhongdian (ZD)	Temperate	ZD-GL	3	5 (2)	3					
Lijiang (LJ)	Temperate	LJ-PMF	1	5 (4)	3	100°11′45″	26°59′58″	3298	134.2	17.5
Lijiang (LJ)	Temperate	LJ-QMF	1	5 (4)	3					
Lijiang (LJ)	Temperate	LJ-RDF	1	5 (4)	3					
Baoshan (BS)	Temperate	BS-PF	3	5 (2)	3	99°17′25″	25°14′01″	2492	127.2	21
Baoshan (BS)	Temperate	BS-MF	2	5 (3)	6					
Baoshan (BS)	Temperate	BS-GL	2	5 (3)	3					
Mengsong (MS)	Tropical	MS-OMF	2	5 (3)	6	100°28′45″	21°30′50″	1656	164.4	25.7
Mengsong (MS)	Tropical	MS-SMF	1	5 (4)	3					
Mengsong (MS)	Tropical	MS-TP	1	5 (4)	3					
Mengla (ML)	Tropical	ML-RMF	2	8 (8)	6	101°34′34″	21°36′46″	774	207.7	24.7
Doi Mae Salong (DMS)	Tropical	DMS-SMF	3	12 (9)	10					
Doi Mae Salong (DMS)	Tropical	DMS-CR	1	3 (2)	3	99°37′23″	20° 10′06″	1126	211.3	27
Doi Mae Salong (DMS)	Tropical	DMS-BMF	1	4 (3)	3					
Doi Mae Salong (DMS)	Tropical	DMS-RMF	1	3 (2)	3					

monoculture pine plantation), an increase in plot size from 100 m^2 to 400 m^2 did not significantly increase the percentage of species richness captured. Whereas in all other land use systems, regardless of whether they were tree-based agricultural systems (maximum three different tree species per plot) or mixed forests, 100 m^2 plots represented < 20 % of the species richness found in the 10 000 m^2 plot. Increasing the plot size in these systems to 400 m^2 significantly increased the percentage of species richness captured (Fig. 1). However, the 400 m^2 plot size still only represented <40 % of the richness observed in 10 000 m^2 for tree-based agricultural systems and mixed forests in both temperate and tropical areas. For grassland systems, even the increase from 100 m^2 to the maximum sampling area of 10 000 m^2 did not lead to a higher estimate of species richness. However, for all investigated land use systems that included trees, an increase in plot size from 100 m^2 to 10 000 m^2 significantly increased recorded species richness ($p \leq 0.05$). These results indicate that the effect of increasing plot size on captured species richness differed between land use systems.

Across all land use systems, for all sampled plot sizes (100 m^2, 400 m^2, and 10 000 m^2), we found that species richness in grasslands was significantly lower than species richness in mixed forests (Table 3). Whereas, comparing tree-based agricultural systems with mixed forests in tropical areas, no significant differences in species richness were recorded between any of the plot sizes (Table 3). When comparing species richness amongst different plot sizes for different land use systems, we found that the species richness significantly increased when the plot size was increased from 100 m^2 to 10 000 m^2, except for tree-based agriculture (Table 3). These findings indicate that despite the strong influence of plot size on species richness, the qualitative comparability between land use systems of the same size was not affected. Thus, depending on the objective of the study, smaller plots sizes might be sufficient, when aiming at a qualitative comparison, whereas to quantitatively capture absolute species richness, larger plot sizes are required.

Previous quantitative studies regarding macrofungi have incorporated different plot sizes, ranging from 100 m^2 to 10 000 m^2 (Baptista et al., 2010; Henkel et al., 2012; O'Hanlon and Harrington, 2012a, b; Zhang et al., 2010). O'Hanlon and Harrington (2012a) suggested that 100 m^2 plots could obtain up to 80 % of macrofungal species richness in a homogenous forest area (Scots pine and Norway spruce forests from England). Our findings indicate that forest type, location, and climate are likely to determine appropriate plot sizes. In monoculture pine forests, 100 m^2 plots contained only 39 % of total macrofungal species richness, and 400 m^2 plots contained 62 % of total species richness (Fig. 1).

Henkel et al. (2012) established 10 000 m^2 plots in a *Dicymbe* monodominant forest, and further 10 000 m^2 plots that were divided into 100 m^2 by 100 m^2 quadrats, to investigate the effect of plot size on capturing macrofungal fruiting body diversity. Their results showed that nearly 80 % of mushroom species were found in 150 (1500 m^2) out of 630 (6300 m^2) quadrats. Although our 10 000 m^2 plots were not fully divided into 100 m^2 plots, we obtained similar results. In the plots from the monoculture pine

Table 2
Study plot information, including land use system and the dominant tree species within each plot.

Plot name	Land use system	Detailed description	Dominant tree species
ZD-CF	Mixed forest	Natural forest with disturbance	*Pinus densata*, *Picea likiangensis*
ZD-MF1	Mixed forest	Natural forest with disturbance	*Rhododendron rubiginosum*, *Lyonia ovalifolia var. hebecarpa*, *Picea likiangensis*
ZD-MF2	Mixed forest	Natural forest with disturbance	*Lyonia ovalifolia var. hebecarpa*, *Rhododendron tapetiforme*, *Betula platyphylla*
ZD-GL	Grassland	Natural grassland with disturbance	No
LJ-PMF	Mixed forest	Natural forest with disturbance	*Pinus armandii*, *Pinus yunnanensis*
LJ-QMF	Mixed forest	Natural forest with disturbance	*Quercus semecarpifolia, Quercus guyavaefolia*
LJ-RDF	Mixed forest	Natural forest with disturbance	*Rhododendron rubiginosum, Rhododendron traillianum,*
BS-PF	Pine monoculture	Pine plantation	*Pinus armandii*, *Pinus yunnanensis*
BS-MF1	Mixed forest	Natural forest with disturbance	*Castanopsis orthacantha*, *Quercus rehderiana*, *Pinus armandii*
BS-MF2	Mixed forest	Natural forest with disturbance	*Quercus rehderiana*, *Pinus yunnanensis*, *Pinus armandii*
BS-GL	Grassland	Natural grassland with disturbance	No
MS-OMF1	Mixed forest	Natural forest with disturbance	*Syzygium brachythyrsum*, *Xanthophyllum flavescens*, *Macaranga henryi*
MS-OMF2	Mixed forest	Natural forest with disturbance	*Cryptocarya hainanensis*, *Myrsine seguinii*, *Anneslea fragrans*
MS-SMF	Mixed forest	Natural forest with disturbance	*Schima wallichii*, *Castanopsis mekongensis Litsea cubeba*
MS-TMP	Tree-based agriculture	Tea plantation	*Castanopsis calathiformis*, *Camellia sinensis var. assamica*, *Castanopsis mekongensis*
ML-RMF1	Mixed forest	Natural forest with disturbance	*Pittosporopsis kerrii*, *Parashorea chinensis*, *Garcinia cowa*, *Mezzettiopsis creaghii*, *Baccaurea ramiflora*, *Knema furfuracea*
ML-RMF2	Mixed forest	Natural forest with disturbance	*Pittosporopsis kerrii*, *Parashorea chinensis*, *Garcinia cowa*, *Mezzettiopsis creaghii*, *Baccaurea ramiflora*, *Knema furfuracea*
DMS-SMF1	Mixed forest	Natural forest with disturbance	*Lithocarpus elegans*, *Castanopsis tribuloides*, *Castanopsis diversifolia*
DMS-SMF2	Mixed forest	Natural forest with disturbance	*Lithocarpus elegans*, *Castanopsis tribuloides*, *Castanopsis diversifolia*, *Castanopsis calathiformis*
DMS-SMF3	Mixed forest	Natural forest with disturbance	*Lithocarpus polystachtus*, *Castanopsis diversifolia*
DMS-CR	Tree-based agriculture	Coffee and rubber plantation	*Hevea brasiliensis*, *Coffea arabica*
DMS-BMF	Mixed forest	Natural forest with disturbance	*Dendrocalamus membranaceous, Erythrina stricta, Heliciopsis terminalis*
DMS-RMF	Mixed forest	Natural forest with disturbance	*Pinus kesiya, Schima wallichii, Albizia odoratissima*

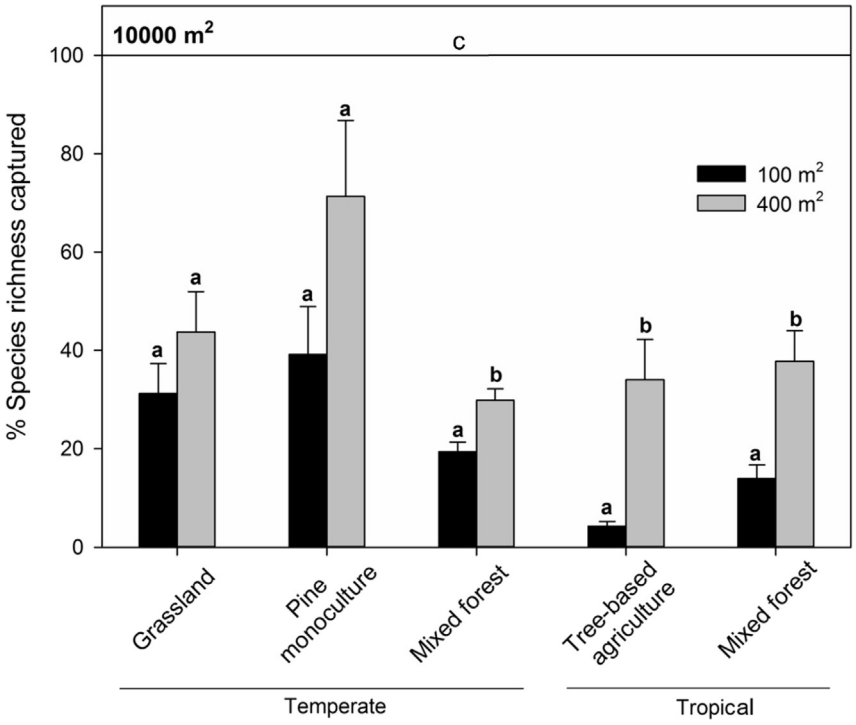

Fig. 1. Species richness expressed as the relative mean percentage of the species richness in 100 m^2 and 400 m^2 subplots against the largest sampling plots (10 000 m^2), for different land use systems, based on sampling data of 2014. Plots lacking 100 m^2 and 400 m^2 subplots were excluded from the analysis, namely all data from ML or 2013. Letters indicate a significant difference ($p \leq 0.05$, Mann-Whitney rank sum test) between median percentage species richness of 100 m^2 and 400 m^2 plot sizes within one land use system. Error bars show standard error of the arithmetic mean. All land use systems present at a site were included in the study, as not all types were present at all sites, the number of replicates differed between land use systems: Grassland: 100 m^2 subplots n = 6 (3 in ZD; 3 in BS), 400 m^2 subplots n = 10 (5 in ZD; 5 in BS); Pine monoculture: 100 m^2 subplots n = 3 (3 in BS), 400 m^2 subplots n = 5 (5 in BS); Mixed forest temperate: 100 m^2 subplots n = 24 (9 in ZD; 9 in LJ; 6 in BS), 400 m^2 subplots n = 30 (10 in ZD; 15 in LJ; 5 in BS); Tree-based agriculture tropical: 100 m^2 subplots n = 6 (3 in MS; 3 in DMS), 400 m^2 subplots n = 8 (5 in MS; 3 in DMS); mixed forest tropical: 100 m^2 subplots n = 27 (9 in MS; 3 in ML; 15 in DMS), 400 m^2 subplots n = 36 (10 in MS; 8 in ML; 18 in DMS).

forest, around 70 % of macrofungal species richness were found within an area of 1200 m^2. From our results we can conclude that to best represent the absolute richness of macrofungal species in all our land use systems, a large plot area (10 000 m^2) is required. However, if the aim of a study were to be a qualitative comparison of different land use systems, smaller plot sizes (100 m^2) would be sufficient.

3.2. Most abundant genera in different plot sizes

In addition to species richness, the abundance of species and genera is an important factor to be considered in macrofungal studies (Baptista et al., 2010; Smith et al., 2002), especially when considering economic value of macrofungi (He et al., 2011; Yang et al., 2012). The homogenous or monoculture systems (grassland and tree-based agriculture) consistently (i.e. over all subplot sizes) obtained a most abundant genus match of ≥50 % with the corresponding 10 000 m^2 plot. For mixed forest systems in temperate and tropical climates, a match of 50 % could only be reached in the largest subplots sampled (400 m^2) (Table 4). Thus, small plot sizes can capture a more representative view of macrofungal species composition in homogenous systems, as opposed to the mixed land use systems. Diverse vegetation cover appears to result in a diverse species composition of macrofungi. In mixed forest systems, the percentage match of abundance increased with increasing plot size, whereas for systems with less diverse vegetation cover, discrete

Table 3
Arithmetic mean of species richness ± standard error for different land use systems and plot sizes in the sampling season 2014. Lower case letters indicate significant differences ($p \leq 0.001$, Mann-Whitney rank sum test) between grassland and mixed forest plots in the temperate study sites as well as between tree-based agricultural systems and mixed forest in tropical regions. Upper case letters indicate significant differences in median species richness between plots sizes ($p \leq 0.05$, ANOVA on ranks) within a single land use system. For Grassland 100 m^2 subplots n = 6 (3 in ZD; 3 in BS), 400 m^2 subplots n = 10 (5 in ZD; 5 in BS) and 10 000 m^2 plots n = 5 (3 in ZD; 2 in BS); For tree-based agriculture 100 m^2 subplots n = 6 (3 in MS; 3 in DMS), 400 m^2 subplots n = 8 (5 in MS; 3 in DMS) and 10 000 m^2 plots n = 2 (1 in MS; 1 in DMS); For mixed forest temperate 100 m^2 subplots n = 24 (9 in ZD; 6 in BS; 9 in LJ), 400 m^2 subplots n = 30 (10 in ZD; 5 in BS; 15 in LJ) and 10 000 m^2 plots n = 10 (5 in ZD; 2 in BS; 3 in LJ); For mixed forest tropical 100 m^2 subplots n = 30 (9 in MS; 6 in ML; 15 in DMS), 400 m^2 subplots n = 36 (10 in MS; 8 in ML; 18 in DMS) and 10 000 m^2 plots n = 10 (3 in MS; 2 in ML; 5 in DMS). "n" represents the number of plots or subplots used in the analysis.

Plot size	Temperate		Tropical	
	Grassland	Mixed forest	Tree-based agriculture	Mixed forest
100 m^2	$4.0 \pm 1.2^{a/A}$ (n = 6)	$19.2 \pm 2.1^{b/A}$ (n = 24)	$2.5 \pm 0.7^{a/A}$ (n = 6)	$7.1 \pm 1.7^{a/A}$ (n = 30)
400 m^2	$5.6 \pm 1.5^{a/AB}$ (n = 10)	$27.5 \pm 2.3^{b/A}$ (n = 30)	$37.9 \pm 11.9^{a/A}$ (n = 8)	$23.0 \pm 3.9^{a/B}$ (n = 36)
10 000 m^2	$11.2 \pm 2.6^{a/B}$ (n = 5)	$102.4 \pm 10.2^{b/B}$ (n = 10)	$72.0 \pm 48.0^{a/A}$ (n = 2)	$55.7 \pm 8.3^{a/C}$ (n = 10)

Note: To analyze the effect of increasing plot size on species richness, data from 2013 was excluded in the analysis as there were no 400 m^2 subplots included in the 2013 survey.

Table 4
Percentage of subplots (100 m^2, 300 m^2 (bulking of three single 100 m^2 plots), and 400 m^2) that had the same most abundant genera of macrofungi as the 10 000 m^2 plot in which the subplots were located. Classed by land use systems and based on sampling data of 2014. For Grassland 100 m^2 subplots n = 6 (3 in ZD; 3 in BS), 300 m^2 subplots n = 2 (1 in ZD; 1 in BS) and 400 m^2 subplots n = 2 (1 in ZD; 1 in BS); Tree-based agriculture 100 m^2 subplots n = 6 (3 in MS; 3 in DMS), 300 m^2 subplots n = 2 (1 in MS; 1 in DMS) and 400 m^2 subplots n = 2 (1 in MS; 1 in DMS); for Mixed forest temperate 100 m^2 subplots n = 24 (9 in ZD; 9 in LJ; 6 in BS), 300 m^2 subplots n = 8 (3 in ZD; 3 in LJ; 2 in BS) and 400 m^2 subplots n = 8 (3 in ZD; 3 in LJ; 2 in BS); for Mixed forest tropical 100 m^2 subplots n = 23 (9 in MS; 14 in DMS); 300 m^2 subplots n = 7 (3 in MS; 4 in DMS) and 400 m^2 subplots n = 7 (3 in MS; 4 in DMS).

Plot size	Temperate		Tropical	
	Grassland	Mixed forest	Tree-based agriculture	Mixed forest
100 m^2	67 % (n = 6)	29 % (n = 24)	50 % (n = 6)	26 % (n = 23)
300 m^2	100 % (n = 2)	38 % (n = 8)	100 % (n = 2)	29 % (n = 7)
400 m^2	50 % (n = 2)	75 % (n = 8)	50 % (n = 2)	57 % (n = 7)

Note: To assess the composition of most abundant genera in different plot sizes, this data analyzed only those 10 000 m^2 plots that contained 100 m^2 and 400 m^2 subplots. Because of the lack of 400 m^2 subplots, all data in 2013 and ML data in 2014 was excluded from this analysis. In order to obtain more comparative plot sizes, we also calculated macrofungal species richness in three single 100 m^2 (providing a total area of 300 m^2) located inside the 10 000 m^2 plot.

sampling of three smaller plots (100 m^2 each) yielded a better capture of the most abundant species than sampling one continuous subplot of 400 m^2. A study of fish diversity in marine environments (McNeill and Fairweather, 1993) showed that several small plots contained significantly more species than a single large plot. Another study on conservation of endangered plants indicated that the combination of several small areas is a good alternative to a single large area, when attempting to protect plant species richness (Järvinen, 1982). Furthermore, a discrete distribution of sampling subplots captures a larger variety of abiotic factors and thereby increases the likelihood of matching the most abundant genera with the main plot. We found that when sampling macrofungi in one forest type within the same area, quadrats arrayed in a regular, but noncontiguous grid were the optimal sampling method.

3.3. *The effect of the number of sampling seasons on capturing species richness*

Macrofungi do not only exhibit a strong heterogeneity in their spatial distribution, but also in their seasonality, with fluctuations in species richness from one season to the next (Fernández-Toirán et al., 2006; Straatsma et al., 2001). Thus, the number of sampling seasons included in a study affects the choice of the correct plot size. Across all our land use systems and plot sizes, we found that a higher macrofungal species richness was captured in two sampling seasons (2013 and 2014 data combined) than in a single season of sampling (Fig. 2A), illustrating temporal fluctuations in the occurrence of macrofungi. Past studies, conducted over a period of 18–31 y, have shown interannual variability in the phenology of macrofungal productivity (Büntgen et al. 2013, 2015). However, the results from our study are very limited due to the low number of sampling seasons included in our dataset. Our results go as far as to show that seasonal variability occurs, but do not allow any strong conclusions to be made. However, there are past studies based on a higher number of sampling seasons which have found similar patterns to our dataset, for example, Henkel et al. (2012) found a strong variation in annually observed ectomycorrhizal macrofungi richness over the course of seven years. However, their first sampling season found 80 % of the total ectomycorrhizal species richness found over the course of the following seven sampling seasons (three subplots of 1 ha each). In our study, in the 2013 sampling season we captured 69–72 % of the total species richness and the 2014 sampling season 43–51 %. These results highlight the variation in macrofungal richness between years and underline the importance of sampling over more than one season to avoid the risk of inadvertently sampling in a year with low macrofungal occurrence. Nevertheless, the role of seasonal variation as a factor needs be considered when designing a study.

However, when also accounting for plot size, we found that by sampling large plots (10 000 m^2) in a single year, the species richness captured was significantly higher or similar to the species richness captured in smaller plots (100 m^2 and 300 m^2 respectively) over two seasons (Fig. 2B). Similarly, the species richness captured in 100 m^2 plots over two seasons was significantly smaller than the species richness captured in 300 m^2 plots in a single season of sampling (Fig. 2C). Thus, despite the strong seasonal

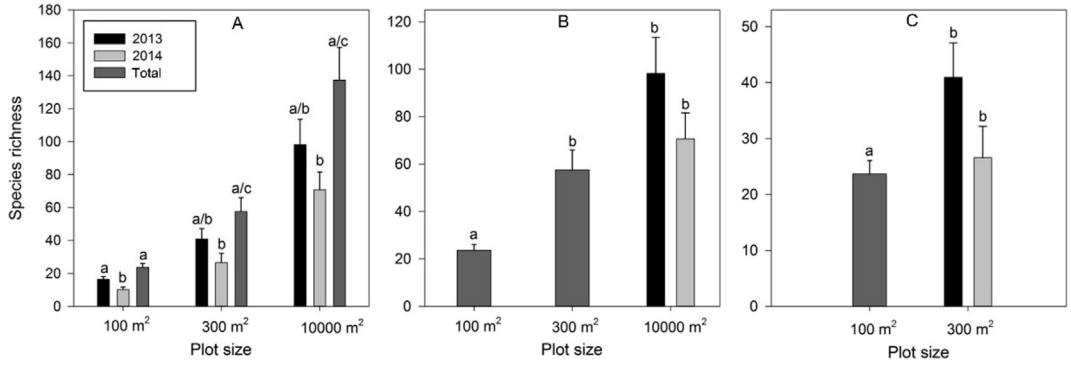

Fig. 2. (A) Species richness within differing plot sizes in 2013, 2014, or the two years combined (Total). (B) Species richness across two seasons in subplots of 100 and 300 m^2 compared to the whole 10 000 m^2 sampling area. (C) Median species richness across two seasons within 100 m^2 versus 300 m^2 subplots. Letters indicate significant differences in species richness ($p \leq 0.05$, ANOVA on ranked data) between plot sizes. Error bars represent standard error of the mean, sample size varied according to plot size: 100 m^2 subplots n = 54 (9 in ZD; 9 in LJ; 6 in BS; 9 in MS; 6 in ML; 15 in DMS) and for 300 m^2 subplots n = 18 (3 in ZD; 3 in LJ; 2 in BS; 3 in MS; 2 in ML; 5 in DMS) and for 10 000 m^2 plots n = 18 (3 in ZD; 3 in LJ; 2 in BS; 3 in MS; 2 in ML; 5 in DMS). Note: All the data in mixed forest collected in 2013 and 2014 was included in this analysis. In order to obtain more comparative plot sizes, we also calculated macrofungal species richness in three single 100 m^2 (total area is 300 m^2) located inside 10 000 m^2.

effect that we observed, a smaller sampling area cannot be compensated for by an additional sampling season, although we could assume that as more sampling seasons are included in a study, this marked effect of plot size versus the number of sampling seasons would diminish. Furthermore, this effect may vary from one study to the next depending on land use systems, selected plot sizes, and duration of the study. Schmit et al. (1999) drew the opposite conclusion to our study from an investigation of macrofungal species richness in two 0.1 ha plots in an oak forest over 2 y: the authors reported that a higher species richness was captured by two sampling seasons in just one 0.1 ha plot compared to one sampling season in 0.2 ha. However, Schmit et al. (1999) doubled their sampling area, whereas we increased the study area by a factor of 100, which should give more robust results. In addition, when comparing a single sampling season using a 300 m^2 plot and two sampling seasons using 100 m^2 plots (plot size increased by a factor of 3) we still observed a significantly higher species richness in the larger plots than could be captured by two sampling seasons in the smaller plots. Therefore, our results indicated that a larger area in a single sampling season would be more accurate than a smaller area assessed over two sampling seasons. However, it is difficult to draw broad conclusions from this comparison, as our data was limited to only two sampling seasons. Nevertheless, some studies investigating species richness of macrofungi have found that species richness varied with more sampling seasons and larger plot sizes. Villeneuve et al. (1989) set up a 400 m^2 permanent plot in each of two forest types (deciduous forest and conifer forest) to evaluate macrofungal diversity in two sampling seasons. They found that the first season captured an average of 75 % of the total number of taxa. In a study conducted over seven sampling seasons, Henkel et al. (2012) found that the first season of sampling captured 80 % of the macrofungal species richness in their 10 000 m^2 plots. Overall, it appears that increasing plot size for a single sampling season can still capture a high proportion of actual species richness.

3.4. Data limitation

Although our study did not have the goal of determining the effect of plot shape, previous studies have reported that the relationship between plot shape and the measurement of species diversity (Myers and Chapman, 1953; Kunin, 1997; Keeley and Fotheringham, 2005), using square (Pradhan et al., 2013), rectangular (O'Hanlon and Harrington, 2012b) and circular plots (Smith et al., 2002) in macrofungal sampling design. For example, Kunin (1997) found that species number in elongated plots is significantly more than that in square plots, however, Keeley and Fotheringham (2005) didn't find the evidence that plot shape affected on species richness. Nevertheless, square and rectangular plots have been the dominant choice (Smith et al., 2002; O'Hanlon and Harrington, 2012b). One of main considerations of plot shape is the effect of trampling. A study conducted by Egli et al. (2006) found that although trampling significantly reduced mushroom production, it did not affect the diversity of mushrooms within a given plot. Nevertheless, it is necessary to avoid trampling effect. A final limitation in our dataset is that our sampling was conducted over two seasons, and although this is a very short period and makes it difficult to draw any form of long term conclusions, it still provides insight into seasonal variability, adding to the evidence already provided by studies conducted over longer periods of time.

4. Conclusion

The results of our investigation indicate that despite the strong influence of plot size on the determination of species richness, the qualitative comparability between land use systems of the same plot size was not affected. Thus, depending on the objective of the study, smaller plot sizes could be sufficient for a qualitative comparison, whereas to quantitatively capture absolute species richness, larger plot sizes are required. Whether macrofungi were sampled in either one or two seasons was less important than plot size to forming estimates of species richness.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.funbio.2018.03.004.

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