

RESEARCH ARTICLE

Does over-dominance of *Bambusa bambos* (L.) Voss. alter abundance and richness of Arbuscular Mycorrhizal fungal community in forests?

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Abstract: Tropical Moist Evergreen forests (TMEF) are the major forest type in the Intermediate Climatic Zone of Sri Lanka. Some of these forests are heavily dominated by a native bamboo species, *Bambusa bambos* (L.) Voss. altering the hierarchical status and structure. The study evaluated whether the over-abundance of *B. bambos* has modified the arbuscular mycorrhizal fungal (AMF) communities in soil. Soil samples collected from bamboo-dominated (BM) and non-bamboo (NB) forest patches in three different locations viz., Moragolla, Maragomuwa and Galboda, were enumerated for AMF spores using wet sieving and decanting method. A total of 1,577 and 898 AMF spores were documented from BM and NB forest patches, respectively. A total of 14 different morphotypes belonged to the genera, *Glomus*, *Scutellospora*, *Gigaspora* and *Acaulospora*, were identified. *Glomus* was the dominant genus in all study sites, while *Acaulospora* the least. The mean abundance and richness of AMF spores were higher in BM than in NB, with the most notable difference observed at Maragomuwa. The site-specific variations may perhaps due to the differences in vegetation characteristics, edaphic properties and disturbance regimes. However, the community structure of AMF showed no conspicuous modifications due to the over-abundance of *B. bambos*. The findings reiterated the general understanding that any changes to the above-ground vegetation may incur impacts on the AMF. However, AMF community structure shows resilience to influences imposed by the dominance of a single species.

Keywords: Over-dominance, *Bambusa bambos*, arbuscular mycorrhizal fungi, Tropical Moist Evergreen Forests, Sri Lanka.

INTRODUCTION

In recent years, soil microbial communities and their participation in ecosystem functions received renewed interests from scientists. Studies confirm a closer link between the above- and below-ground communities, thus any alterations to the vegetation may incur significant changes to the soil microbial community (Grayston *et al.*, 2004; Sun *et al.*, 2016). Invasion by exotic plants is considered as the one of the main contributory factors to bring about changes in vegetation (McDowell and Allen, 2015). The invasion-driven changes to the vegetation have

in turn altered the below-ground parameters including the soil microbiota (Vila *et al.*, 2011; Rodriguez *et al.*, 2015; Yang *et al.*, 2016), perhaps through changes in litter quality and quantity, soil moisture and temperature, root exudates and nutrient turnover rates (Ehrenfeld, 2010). The studies show that the invasion of exotic bamboos sustain significant impacts on the structure and diversity of soil microbial communities, with more emphasis on bacteria (Chang and Chiu, 2015; Lin *et al.*, 2014) than that of fungi (Xu *et al.*, 2015; Li *et al.*, 2017). Of the many fungal groups present in soil, Arbuscular mycorrhizal fungi (AMF) play a vital role in maintaining the composition and diversity of natural and semi-natural ecosystems. AMF show facilitative effect on the invasion success of some exotic plants (Edirisinghe and Madawala, 2017) while others show that AMF could transform habitats to resist invasion (Yang *et al.*, 2016; Zhang *et al.*, 2010), through positive/negative plant-AMF feedback.

In the recent past, scientists have noted that even some native species display an ability to expand their populations, altering the dominance hierarchies of resident forests (Larperkern *et al.*, 2011). Based on the relatively known impacts of exotic plant invasions, it is correct to assume that over-abundance of native plants may also incur similar influences on the soil microbiota, especially when the focal species show properties in contrast to the previously dominant species. Population expansion of moso bamboo (*Phyllostachys pubescens*) in broad-leaved native forests in China has markedly declined the richness and diversity of the vegetation while inducing shifts in the soil fungal community further corroborating the intimate link between the soil fungi and vegetation (Bai *et al.*, 2013; Peay *et al.*, 2013; Chang and Chiu, 2015; Qin *et al.*, 2017).

Bambusa bambos, a native bamboo species, expands populations in some parts of their resident forests in Intermediate and Dry Climatic Zones of Sri Lanka, altering the structure and composition of forest communities. Due to its thorny nature, the economic value of *B. bambos* is relatively low in comparison to other bamboo species present in the island. Until now, few studies have been undertaken to explore the immediate impacts on the above-

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and below-ground communities following the dominance of *B. bambos* in native forests in Sri Lanka (Wijewickrama *et al.*, 2017). The current study investigated whether the over-dominance of *B. bambos* has the potential to alter the abundance, composition and richness of AMF communities in these native forests.

MATERIALS AND METHODS

Site Description

The study was carried out at Moragahakanda area in the Central Province of Sri Lanka. Lately, Moragahakanda

experienced major land use changes due to the construction of a dam across the river Amban, one of the main tributaries of the river Mahaweli, for irrigation and power generation purposes. The area is under the Intermediate Climatic Zone and IM3 Agroecological Zone. Tropical Moist Evergreen Forest (TMEF) is the most prevalent forest type in the area, with *Mangifera zeylanica*, *Canarium zeylanicum*, *Filicium decipiens*, *Dimorcarpus longan*, *Nothopegia beddomei* and *Girroniera parvifolia* as dominant species (Gunatilleke *et al.*, 2008). The mature forests have more or less a continuous canopy with relatively sparse ground vegetation. The altitude is approximately 200 m above sea level. The topography of the area, shaped by the Knuckles Mountain

Table 1: Basic soil characteristics at bamboo-dominated (BM) and non-bamboo (NB) forest patches in Galboda, Maragomuwa and Moragolla sites, Sri Lanka.

	Study Sites					
	Galboda		Maragomuwa		Moragolla	
	BM	NB	BM	NB	BM	NB
Maximum Canopy height (m)	15	20	12	12	15	20
Stem Density (per ha)	2,744	2,955	5,106	4,494	1,866	2,606
#Soil Mineral Fractions (%)						
Sand	40	38	33	32	37	40
Silt	33	41	37	49	37	35
Clay	25	21	28	19	26	24
#Soil pH	6.1 ^{bc}	5.9 ^{bc}	6.3 ^{ab}	6.2 ^{ab}	6.5 ^a	5.9 ^c
#Soil Moisture (%)	15.0	18.0	20.1	25.0	12.4	13.6

#Soil parameters were statistically analyzed using General Linear Model (GLM) and significant differences were only indicated using different upper case letters. GLM: Mineral Fractions: $F = 0.01$, $p = 0.913$; Soil pH: $F = 19.35$, $p \leq 0.000$; Soil Moisture (%): $F = 2.67$, $p = 0.108$.

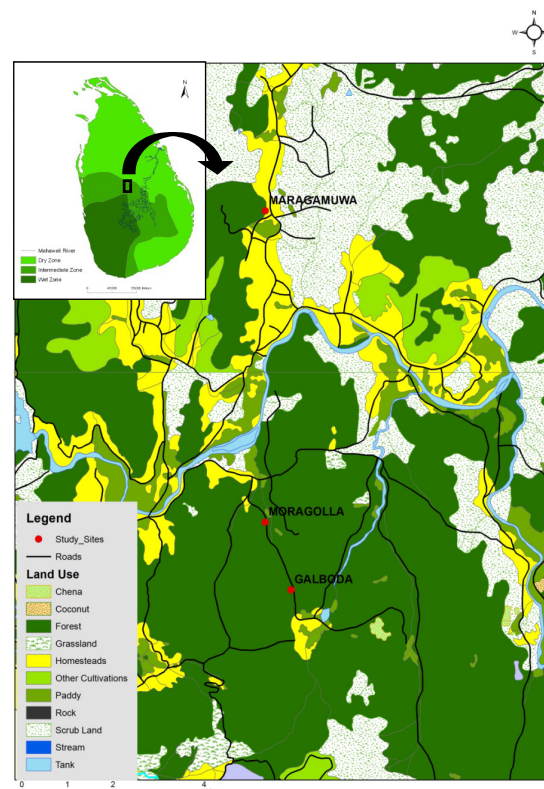


Figure 1: A land use map showing the three study sites (Moragolla, Maragomuwa and Galboda) located at Moragahakanda area close to the northern boundaries of the Intermediate Zone of Sri Lanka.

Range, is classified as flat to gentle slopes (IUCN 2007). The mean annual rainfall is ranged from 1,750 to 2,500 mm. The area receives rainfall from both north-eastern and south-western monsoons, with the bulk receiving from the latter. A short and less prominent dry season is experienced in the middle of the year. The mean annual temperature is ranged between 22.5° – 25.0 °C. The geology of the area is belonged to the Highland Series from the pre Cambrian era with reddish brown earths and immature brown loams as the major soil types (Somasekaram 1988).

Three representative TMEF forest patches, situated approximately 2 – 6 km apart and more or less equally dominated by bamboo (BM), were selected for the study viz., Galboda (GAL), Moragolla (MOR) and Maragomuwa (MAR) (Figure 1). Three comparable forest patches devoid of bamboo, hereafter will be known as non-bamboo (NB) forest patches, located close to their corresponding BM patches were also selected for comparison. The stand characteristics and some basic soil parameters of the study sites are given in Table 1. *Bambusa bambos* (Poaceae) dominated in BM forests while *Dimocarpus longan* (Sapindaceae) was in NB forest patches.

Sampling, extraction and identification of AMF spores

Soil samples were collected from the top soil layer (0 - 10 cm) from each study site using a spade at the end of a wet period during April and May, 2017. The 0 – 10 cm soil layer generally records the highest number of AMF spores compared to layers deeper down (Shukla et al., 2013). Each soil sample is a composite of three sub-samples taken from an area of approximately 1 m radius. From each BM and NB sites, 10 such composite soil samples were collected, totaling 60 samples in all study sites. The soil samples were kept in sealed and labeled polythene bags and stored in a refrigerator (at 4 °C) until further analysis. From each sample, 100 g of soil was used to extract AMF spores using the wet sieving and decanting method, followed by sucrose centrifugation using a set of sieves of different mesh sizes viz., 125, 63 and 45 µm (Sieverding, 1991). The spores were counted and identified into different morphotypes under 100 – 400× magnification using a stereomicroscope. The representative spores from each morphotype were mounted on slides using alcohol lacto-glycerol (PVLG) and identified to their generic level using spore characteristics given in INVAM website (<http://invam.caf.wvu.edu>). The spore density is the number of spores in 100 g of fresh soil. The species richness (number of spore morphotypes in 100 g fresh soil), relative abundance [(total number AMF spores belonging to each genera or spore size category/ total number of spores) × 100] and Shannon-Wiener Diversity Index (H') were also calculated. The mean abundance (average number of spores per 100 g fresh soil) and richness (average number of different morphotypes per 100 g fresh soil) of AMF spores were also determined.

Though conventional methods of enumeration and identification of AMF spores are known to be subjective, time-consuming and laborious, the recent published work proves that these conventional methods are still been widely used by the scientists for their simplicity and reliability (Zhang et al., 2016; Willis et al., 2016; Zubek et al., 2016).

Sharma and Buyer (2015) compared conventional methods (wet sieving followed by microscopic observation) with that of lipid biomarker analyses and produced comparable results, further endorsing the validity of these methods.

Statistical Analysis

The General Linear Model (ANOVA:GLM) was performed to determine any significant effects of locations, dominance status (bamboo-dominated/non-bamboo), spore size (125, 63 and 45 µm) and their respective interactions on the density and richness of AMF spores. Before using ANOVA, the data set is checked for normality of distribution. Mean separations were done using Tukey HSD at alpha = 0.05. Soil parameters (soil moisture, soil pH and mineral fractions) were also analyzed statistically using GLM. All analysis was performed using Minitab 16.0 statistical software.

RESULTS

The wet sieving has yielded 1,577 and 898 AMF apparently live spores in BM and NB sites, respectively. Moragolla has recorded the highest number of AMF spores (964) followed by Maragomuwa (797) and Galboda (714). In all three study sites, bamboo-dominated (BM) forest patches recorded comparatively higher abundance of AMF spores in comparison to non-bamboo (NB) forests (Table 1). Of the totals (1,577 and 898), 36, 34 and 30 % and 33, 30 and 37 %, of spores were categorized into 125, 63 and 45 µm spore size categories, in BM and NB respectively. A total of 14 morphotypes of AMF spores were recorded in all study sites, belonging to four families, Glomeraceae, Scutellosporaceae, Gigasporaceae and Acaulosporaceae. Nearly half of the AMF spores were belonged to the family of Glomeraceae in both BM (45 %) and NB (50 %) forests, while the lowest contribution was recorded from Acaulosporaceae (7.5 and 6.6% in BM and NB, respectively).

Of the 14 morphotypes, three morphotypes were belonged to the genera *Acaulospora* and *Scutellospora* each and four morphotypes from *Gigaspora* and *Glomus* each. The diversity indices showed comparatively higher values in BM over NB forest patches in all study sites, except at Maragomuwa. The evenness values close to 1.0 indicate that AMF spores are distributed more or less evenly in all study sites, irrespective of the presence or absence of bamboo.

Table 2: Abundance, richness, S-W Diversity and evenness indices of bamboo-dominated (BM) and non-bamboo (NB) forest patches at Moragolla, Maragomuwa and Galboda sites, Sri Lanka.

Study Site	Total number of AMF spores (per kg soil)	Total Number of morphotypes (per kg soil)	Shannon-Wiener Diversity Index (H')	Evenness
Moragolla				
BM	563	12	2.250	0.905
NB	401	12	2.204	0.887
Maragomuwa				
BM	602	12	2.201	0.886
NB	195	12	2.205	0.887
Galboda				
BM	412	14	2.446	0.927
NB	302	14	2.353	0.892

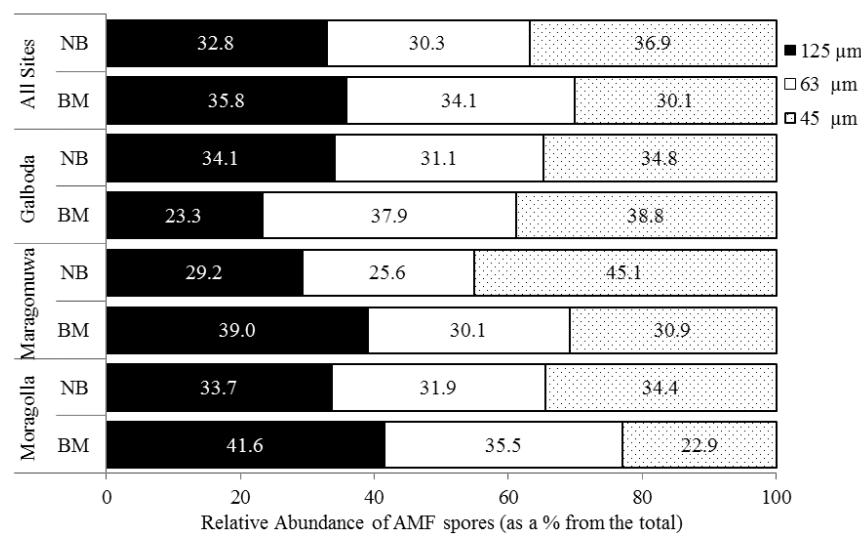


Figure 2: Relative abundance of AMF spores (as a percentage from the total number of spores) classified under different size categories (125, 63 and 45 μm) in bamboo-dominated (BM) and non-bamboo (NB) forest patches in Moragolla, Maragomuwa and Galboda sites, Sri Lanka.

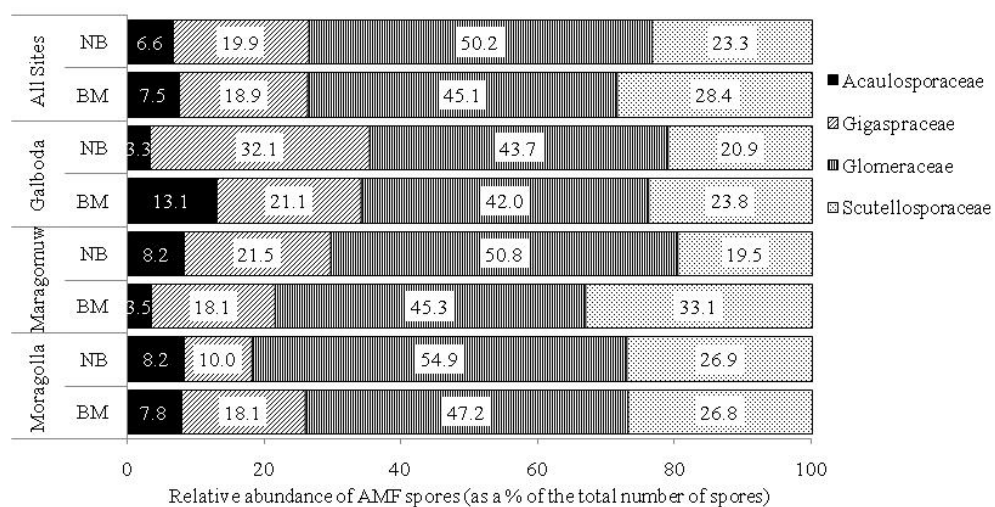


Figure 3: Relative abundance of AMF spores (as a percentage from the total number of spores) classified under different families in bamboo-dominated (BM) and non-bamboo (NB) forest patches in Moragolla, Maragomuwa and Galboda sites, Sri Lanka.

The relative abundances (RA) of AMF spores belonging to three size categories and four genera were more or less similar between study sites irrespective of bamboo over-dominance (Figures 2 and 3). In all forest patches, the family Glomeraceae recorded a higher RA of spores (42 – 55%), followed by Scutellosporaceae and Gigasporaceae (Figure 3). The lowest contribution of AMF spores was reported from the family Acaulosporaceae (3 – 13 %). However, no distinct patterns were observed in RAs between BM and NB forest patches. In all study sites, 3 - 4 morphotypes, mainly of the genus *Glomus*, have contributed to 50 % of the total RA, further highlighting

the dominance of *Glomus*.

The mean abundance of AMF spores was significantly higher in BM forest patches in comparison to NB in both Maragomuwa and Moragolla sites, with a more striking difference in the latter (GLM: $F = 24.15$, $p \leq 0.001$; Figure 4). The BM forests at Maragomuwa also demonstrated a significantly higher AMF spore richness in comparison to NB forest patch (GLM: $F = 9.16$, $p = 0.004$), with no such difference reported in other two sites.

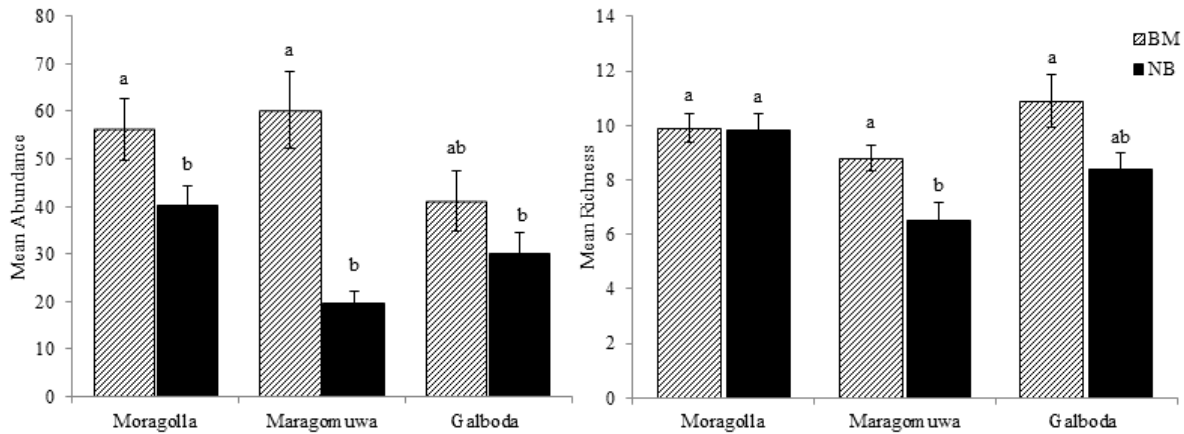


Figure 4: Mean abundance and richness of AMF spores (per 100 g fresh soils) in bamboo-dominated (BM) and non-bamboo (NB) forest patches in Moragolla, Maragomuwa and Galboda sites, Sri Lanka. Significant differences are indicated using different lowercase letters. Vertical bars represent standard error of means (SEM).

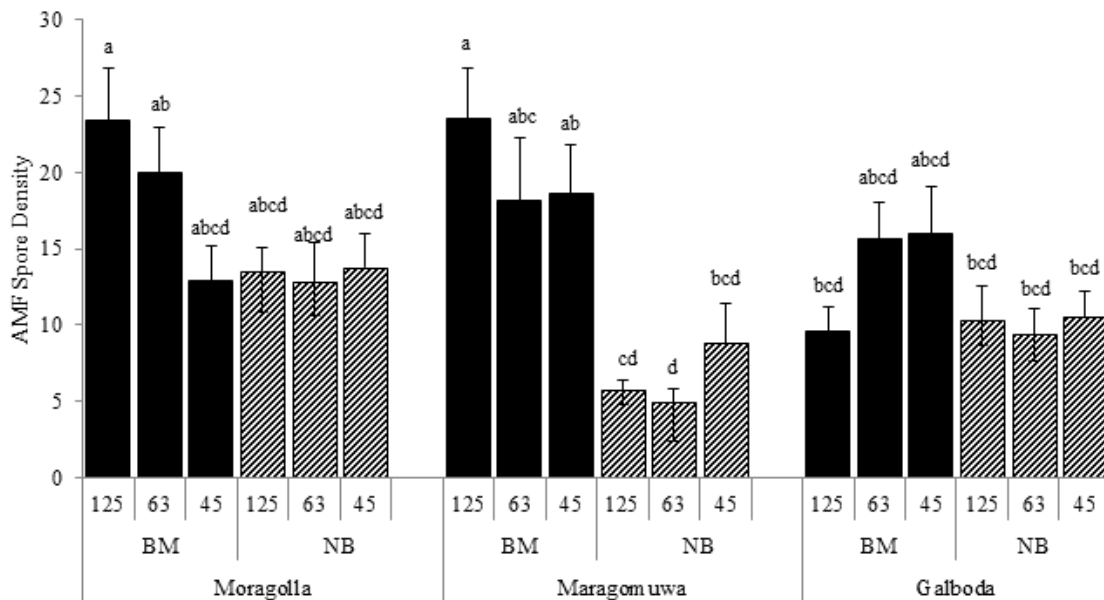


Figure 5: AMF spore density (per 100 g fresh soils) categorized into different size categories (125, 63 and 45 m) in bamboo-dominated (BM) and non-bamboo (NB) forest patches in Moragolla, Maragomuwa and Galboda sites, Sri Lanka. Significant differences are indicated using different lowercase letters. Vertical bars indicate standard error of means (SEM).

Table 3: Statistical parameters following the analysis of mean abundance and richness of AMF spores using General Linear Model (GLM). Significant differences between parameters and their interactions are indicated as ‘*’ $p \leq 0.05$, ‘**’ $p \leq 0.001$ and ‘***’ $p \leq 0.001$ and ‘ns’ not significant.

Source of Variation	DF	F value	P
Site (MOR/MAR/GAL)	2	4.23	0.016*
Dominance (BM/NB)	1	40.13	0.000***
Spore size (45/63/125 μm)	2	0.24	0.787 ^{ns}
Site \times Dominance	2	6.57	0.002**
Site \times Spore Size	4	1.77	0.138 ^{ns}
Dominance \times Spore Size	2	1.33	0.268 ^{ns}
Site \times Dominance \times Spore size	4	1.77	0.137 ^{ns}

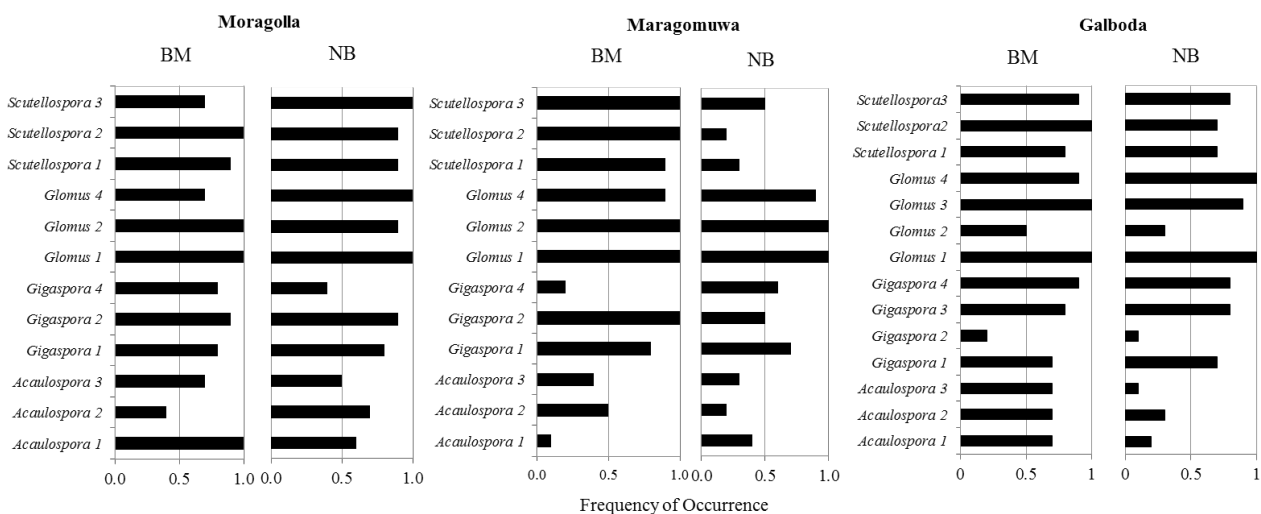


Figure 6: Frequency of occurrence of different AMF spore morphotypes belonging to Acaulospora (3 species), Gigaspora (4 species), Glomus (4 species) and Scutellospora (3 species) in bamboo-dominated (BM) and non-bamboo (NB) forest patches at Moragolla, Maragomuwa and Galboda sites.

At Maragomuwa, the densities of AMF spores belonging to large and medium size categories (125 and 63 μm) were significantly lower in NB than that in BM (Figure 5 and Table 3). The frequency of occurrence of AMF morphotypes was rather similar between BM and NB forest patches at Moragolla, but more distinct differences were recorded in Maragomuwa. The *Acaulospora* and *Scutellospora* spores were more frequent in BM than in NB at Galboda and Maragomuwa, respectively. Also, one *Gigasporasp.* (*Gigaspora* 3) was recorded exclusively in both BM and NB forest patches at Galboda, while all other morphotypes shared among sites (Figure 6).

DISCUSSION

Any modifications to the above-ground vegetation may impose significant impacts on the soil microbiota due to their high inter-dependence (Hooper *et al.*, 2000). A preliminary vegetation survey has shown that the over-dominance of *B. bambos* has incurred compositional changes in TMEF forests in Sri Lanka (Wijewickrama *et al.*, 2017). The results of the present study showed that the over-abundance of *B. bambos* has increased the abundance and richness of AMF spores, with few site-specific contrasts possibly due to inherent differences in terms of vegetation,

edaphic parameters and on-going disturbances (natural and anthropogenic) between study sites. Previous studies have also demonstrated that the abundance and diversity of soil microbes could increase following invasion of exotic bamboos despite the reduced plant diversity in native forests in China (Xu *et al.*, 2015; Qin *et al.*, 2017). In contrast, Li *et al.*, (2017) observed a reduced abundance and modified community composition in fungi following a bamboo invasion, discouraging generalization of potential impacts. Though some AMF are known to be host specific (Alguacil *et al.*, 2011; Martinez-Garcia *et al.*, 2015), few species have the ability to colonize wide range of host species (Öpik *et al.*, 2006). This explains how above- and below-ground communities may alter according to the ‘Driver/Passenger Hypothesis’, with plants driving AMF communities and *vice versa* (Hart *et al.*, 2001). Furthermore, other environmental and soil factors may also contribute to any changes in AMF communities (Xu *et al.*, 2015; Li *et al.*, 2017). Soil pH has been identified as one of the crucial parameters responsible for changes in plant and AMF communities (Helgason and Fitter, 2009). Increase of soil pH following bamboo invasion has been reported by many workers (Chang and Chiu, 2015; Umemura and Takenaka, 2015; Pan *et al.*, 2015). In the

present study too, though not significantly always, BM patches had relatively higher pH compared to that of NB, further confirming the link between soil pH and AMF. In addition, other abiotic factors such as available N and P, soil organic matter, soil moisture and temperature may also be responsible for changes in AMF communities, though the parameters are not analyzed in the present study (Li *et al.*, 2015; Hazard *et al.*, 2013; Qin *et al.*, 2015; Qin *et al.*, 2017; Sun *et al.*, 2013).

The present study has recorded relatively low AMF spore densities (19 - 60 AMF spores per 100 g soil) in contrast to numbers obtained in different forest types in other regional countries including Sri Lanka (Mafaziya and Madawala, 2015; Madawala, 2014; Chandrasekera *et al.*, 2005; Jefwa *et al.*, 2009; Belay *et al.*, 2015). The lower numbers in the present study may perhaps be due to low sporulation events during the time of the sampling. Edaphic and environmental properties, together with the different vegetation and natural and anthropogenic disturbances may also have contributed to relatively low spore counts (Mafaziya and Madawala, 2015). The AMF spore abundance shows an inverse relationship with that of the soil moisture (Shukla *et al.*, 2013; Bouamri *et al.*, 2014). In the present study, the soil samples were collected at the end of a wet period, perhaps explaining the low numbers of AMF spores.

The results suggest that the over-abundance of *B. bambos* did not change the composition and structure of AMF communities, reiterating the resilience of AMF communities to disturbances (Urcelay *et al.*, 2009; Xiang *et al.*, 2015). In the present study, the genus *Glomus* represented approximately 50% of the total AMF spores in all study sites, irrespective of the dominance of *B. bambos*. *Glomus* and *Acaulospora* species usually produce more spores than that of *Gigaspora* and *Scutellospora* (Holste *et al.*, 2016), thus favouring the fact that smaller spores are faster in production than that of larger spores (Hepper, 1984). *Glomus* is also a known host generalist, with the potential to colonize a range of plants (Börstler *et al.*, 2008). Moreover, *Glomus* is better adapted to disturbances due to their high sporulation rates and colonizing potentials (Daniell *et al.*, 2001). Others suggest that *Glomus* can be more dominant in high organic soils (Lekberg *et al.*, 2007), while *Gigaspora* and *Scutellospora* with extensive extraradical hyphal growth and nutrient acquisition power may favour low fertile soils (Hart and Reader, 2002; Maherali and Klironomos, 2007). However, with the ability to produce relatively smaller spores, *Acaulospora* still showed the least dominance in all study sites in the present study.

The results suggest that the 30 – 40 years of over-abundance of *B. bambos* (based on the communications from the villagers in peripheral hamlets) has shown the potential to increase the mean abundance and richness of AMF but with no compositional modifications in their AMF communities. However, previous studies have demonstrated compositional changes in AMF communities following invasion by exotic species (Yang *et al.*, 2016) while others reiterated their resilience to such disturbances

(Carey *et al.*, 2015). These conflicting findings may perhaps be due to the ability of AMF communities to revert back to their initial state so rapidly following immediate responses to changes in vegetation (Lankau, 2011; Carey *et al.*, 2015). Studies also revealed that seasonal and/or annual compositional changes could also be observed in AMF communities due to changes in biotic and abiotic factors (Docherty *et al.*, 2012; Frenk *et al.*, 2014). In the present study, the soils were sampled only once, thus making it difficult to capture any seasonal/annual changes to the composition of the AMF communities.

CONCLUSION

The results show the potential of increasing the abundance and sometimes even richness of AMF following the dominance of *B. bambos*. However, the AMF community structure seems unaffected indicating their resilience to above-ground changes. In order to capture seasonal changes of AMF communities, more frequent and intense sampling is recommended.

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