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ORIGINAL ARTICLE

Arbuscular mycorrhizal fungal communities along a pedo-hydrological gradient in a Central Amazonian terra firme forest

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Abstract Little attention has been paid to plant mutualistic interactions in the Amazon rainforest, and the general pattern of occurrence and diversity of arbuscular mycorrhizal fungi (AMF) in these ecosystems is largely unknown. This study investigated AMF communities through their spores in soil in a 'terra firme forest' in Central Amazonia. The contribution played by abiotic factors and plant host species identity in regulating the composition, abundance and diversity of such communities along a topographic gradient with different soils and hydrology was also evaluated. Forty-one spore morphotypes were observed with species belonging to the genera *Glomus* and *Acaulospora*, representing 44 % of the total taxa. Soil texture and moisture, together with host identity, were predominant factors responsible for shaping AMF communities along the pedo-hydrological gradient. However, the variability within AMF communities was largely associated with shifts in the relative abundance of spores rather than changes in species composition, confirming that common AMF species are widely distributed in plant communities and all plants recruited into the forest are likely to be exposed to the dominant sporulating AMF species.

Keywords Amazonia · Arbuscular mycorrhizal fungi · Host specificity · Pedo-hydrological gradient · Spore community composition · Abundance and diversity · Tropical forests

Introduction

Arbuscular mycorrhizal fungi (AMF) are ubiquitous obligate symbionts of the phylum Glomeromycota (Schüßler et al. 2001) which, due to their low host specificity and their broad geographic distribution, associate with the majority of terrestrial plant species (Smith and Read 2008), including almost all trees in species-rich tropical forests (Alexander and Lee 2005). A major challenge in ecology is to understand the factors that influence species distribution and the assemblage of biological communities. The spatiotemporal distribution of biological communities is shaped by deterministic and stochastic processes. The former emphasizes species differences in their responses to abiotic and biotic factors, and the latter highlights the importance of dispersal and other non-deterministic processes. Although the role played by fungal dispersal in determining AMF community structure has been poorly researched (Lekberg et al. 2007; Dumbrell et al. 2010), studies on the effects of soil physical and chemical properties (Brundrett 1991; Fitzsimons et al. 2008), as well as host plant

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(Helgason et al. 2002; Lovelock et al. 2003) and seasons (Pringle and Bever 2002), have shown that deterministic processes play a major role in regulating the composition and structure of AMF communities.

Mycorrhizal fungal communities in an undisturbed tropical forest can be complex and species-rich (Alexander and Selosse 2009), but those in the Amazon rainforest are little described, and therefore the general pattern of AMF occurrence and diversity there remains unknown (Stürmer and Siqueira 2011). Most of the available information relates to AMF community studies (Stürmer and Siqueira 2006, 2011) that rarely associate species composition variability with environmental factors (Peña-Venegas et al. 2007). More research is therefore required to understand how important the complexity of mycorrhizal fungal communities is to tropical forest diversity, productivity and resilience (Alexander and Selosse 2009).

Despite having nutrient-poor and acidic soils, most of Amazonia is covered by the dense lowland evergreen rainforest formation (sensu Whitmore 1984), often referred to as 'terra firme' (or non-flooded) forest. High temperatures and high annual rainfall control the biological activity in tropical forest soil and litter and lead to a rapid nutrient cycling by the soil decomposer community. Floristic differences within terra firme forests have been related to dispersal limitation, to the presence of large geological units, as well as fine-scale environmental gradients (Pitman et al. 2001, 2008; Phillips et al. 2003; Tuomisto et al. 2003; Montufar and Pintaud 2006; Higgins et al. 2011). Soil topographic gradient in particular has long been recognized as an important niche division for plants in Central Amazonian forests (Kahn 1987; Ribeiro et al. 1999; Costa et al. 2005), and recently, fruit body production by the litter decomposing fungi community was also observed to be spatially structured along this gradient (Braga-Neto et al. 2008). Since AMF communities can be shaped by both soil type and plant host species (Vandenkoornhuyse et al. 2002b; Lovelock et al. 2003; Oehl et al. 2010), it is expected that aboveground vegetation differences along a pedo-hydrological gradient are mirrored in the belowground fungal communities.

The objectives of the present study were (1) to characterise AMF spore communities in an Amazonian terra firme forest and (2) to evaluate the contribution played by abiotic factors and plant host species identity in regulating the composition, abundance and diversity of such communities. To do so, soil samples were collected along a gradient over an undulating terrain with different soils and corresponding hydrologic properties, from high-lying areas, characterised by well-drained and nutrient-poor clayey soils, to sandy valley bottoms, with a water table close to the surface. To evaluate the influence of host tree identity on AMF communities, the rhizosphere soil of three leguminous woody species was sampled: *Andira micrantha* Ducke and *Eperua grabriflora* (Ducke) Cowan, both distributed along all the gradient, and *Zygia racemosa* (Ducke) Barneby & Grimes, typically found on plateaux.

Materials and methods

Study site

The study was conducted at the Adolpho Ducke Forest Reserve (RFAD), a protected area of 10,000 ha located 26 km northeast of Manaus (03°00′00″, 03°08′00″ S; 59°52′40″, 59°58′00″ W), Amazonas, Brazil. The region is characterised by an equatorial climate (type Afi by the Köppen system), with a mean annual temperature of 26 °C (minimum, 19 °C; maximum, 39 °C).

Precipitation seasonality at the site is defined by a relatively dry period from June to November, with approx. 100 mm rainfall per month, and a rainy season from December to May. Precipitation varies between 1,900 and 2,300 mm/year, with most of it falling in the rainy season.

The elevation varies from 40 to 140 m a.s.l. Soils are derived from tertiary marine sediments from the Barreiras group and cover plateaux that are more or less strongly dissected by the hydrographic system (Chauvel et al. 1987). Soil type varies along a pedo-hydrological gradient with plateaux characterised by oxisols, slopes by ultisols and valleys (locally known as '*baixios*') by hydromorphic spodosols (Chauvel et al. 1987; de Toledo et al. 2011).

The water table is deep on the plateaux and close to the surface at the valley bottoms that are almost permanently waterlogged during the rainy season (Schietti et al. 2013).

The dominant vegetation type in the Reserve is terra firme-type lowland evergreen primary forest, characterised by a closed canopy of 30–37 m, with emergent trees reaching 45 m and the dominant tree families represented by Fabaceae, Burseraceae, Sapotaceae, Lecythidaceae, Chrysobalanaceae, Moraceae and Lauraceae (Ribeiro et al. 1999). Emergent trees are abundant on the plateaux where the canopy reaches 35–40 m and are scarce on slopes and *baixios* where the canopy reaches 25–35 and 20–35 m, respectively (Ribeiro et al. 1999).

Sampling design and data collection

A sampling grid of 1 × 1 km was used over an area of 25 km^2. The gridlines, 12 trails spaced at a distance of 1 km, six in the direction north–south (NS) and six in the direction east–west (EW), were established by the PPBio Programme (http://ppbio.inpa.gov.br). Five permanent plots (40 × 250 m) were delimited off each trail in an E–W direction along elevation contour lines to minimise variation in topography within a plot (Fig. 1a, b). A total of 30 such permanent plots were sampled.

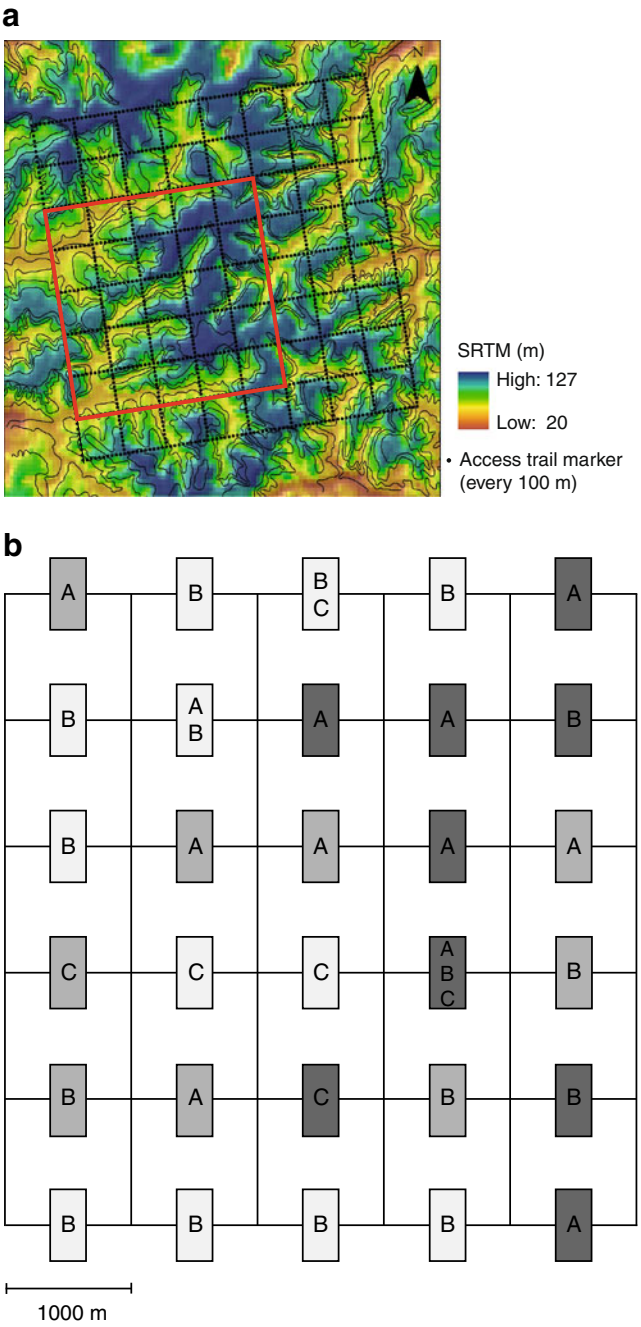

Fig. 1 **a** The Adolpho Ducke Forest Reserve grid system with 72 permanent plots. The *red line* delimits the sampling grid (shown in **b**), established by the PPBio Programme. Coordinates: NW corner—2.927 S, 59.97 W; NE corner—2.917 S, 59.897 W; SW corner—2.999 S, 59.959 W; SE corner—2,989 S, 58.886 W. Contour lines are spaced every 20 m. **b** Sampling grid covering an area of 25 km^2 and characterised by 30 permanent plots (40×250 m, *rectangles*) and 12 trails spaced at a distance of 1 km, six in the NS direction and six in the EW direction. *Letters within the rectangles* represent host species occurrence in the permanent plots: *Z. racemosa* (*A*), *E. grabriflora* (*B*) and *A. micrantha* (*C*). *Grey shades* represent topographic position: *baixio* (*light grey*), slope (*middle grey*) and plateau (*dark grey*)

The maximum difference in elevation was 58 m between the lowest and the highest plots.

The rhizosphere of three tree species belonging to the Leguminosae and known to host AMF (Maciel 2007) were sampled: *A. micrantha*, *E. grabriflora* and *Z. racemosa* (Fig. 1b). *A. micrantha* is occasionally found on Amazonian plateaux, slopes, and *baixios* and belongs to the Papilionoideae subfamily. It is known as sucupira. *E. grabriflora* is frequently distributed in areas of plateau, slope and *baixios* of central and eastern Amazonia. It belongs to the Caesalpinioideae subfamily and is commonly known as muirapiranga and big-leaved muirapiranga. *Z. racemosa* occurs typically on plateaux of the Amazon and Guiana tropical regions and belongs to the Mimosoideae subfamily. It is commonly known as angelim rajado, ingarana and ingarana of terra firme.

A. micrantha, *E. grabriflora* and *Z. racemosa* were sampled in six, 16 and 12 plots, respectively (Fig. 1b). Three individuals belonging to each species (diameter at breast height, 10–30 cm) were chosen in every plot, at least 50 m apart from each other. In all except three of the 30 plots, a single plant host species was sampled. Soil samples were collected in 2006 during the transition between the rainy and dry seasons (June/July). Four soil subsamples were collected using a cylinder (diameter, 6 cm) at the cardinal points of each individual at a depth of 0–10 cm and pooled together. A total of 102 soil samples were collected, air-dried, and used for soil analyses and AMF spore isolation and identification.

Soil analyses

Soil texture was determined by particle size analysis using the pipette method (Gee and Bauder 1986) and soil moisture content by the gravimetric method. Soil pH was determined in 1:1 soil/water (*v*/*v*); available P^+ and K^+ were extracted by Melich 1 and determined colorimetrically and by atomic absorption, respectively. Available Al^{3+}, Ca^{2+}, Mg^{2+}, Fe, Zn^+ and Mn^{2+} were determined using atomic absorption after extraction with 1 N KCl. All the analyses were made in the Laboratório Temático de Solos e Plantas of the Instituto Nacional de Pesquisas da Amazônia following the methodology of EMBRAPA (2009).

AMF spore extraction and species identification

Spores were isolated from a subsample of 50 g of each composite soil sample by wet sieving (Gerdemann and Nicolson 1963), followed by centrifugation in a sucrose solution (Daniels and Skipper 1982). Soil samples were firstly placed in tap water and the soil suspension passed through two nested sieves (710 and 45 μm), after being centrifuged at 1,750 rpm for 5 min. The material collected on the 45-μm sieve was suspended in a sucrose solution (48 %) and centrifuged at 1,750 rpm for 15 s. The

supernatant was decanted and transferred into Petri dishes and the spores inspected under a dissecting microscope.

Intact spores (i.e. undamaged, with cytoplasmic content) were separated by morphotype according to macroscopic features, such as size, colour, hyphal attachment and shape. After counting, the spores were mounted permanently on slides in polyvinyl lactoglycerol (PVLG) and PVLG mixed with Melzer's reagent (1:1, *v*/*v*) for identification based on current species descriptions, identification manuals (Schenck and Perez 1990; Schüßler and Walker 2010) and online reference species descriptions (http://invam.caf.wvu.edu/; http://www.zor.zut.edu.pl/Glomeromycota/Taxonomy.html; http://www.lrz.de/~schuessler/amphylo/amphylo_species.html).

Mounted specimens have been deposited at the Herbário da Universidade Estadual de Maringá, Parana State.

Data analysis

Fungal species accumulation curves with 95 % confidence intervals were generated for each tree species studied using the program EstimateS, version 8 (Colwell 2006). Relative abundance was calculated for each morphotype in each soil sample as the number of AMF spores of that morphotype divided by the total number of AMF spores in the considered soil sample. Relative frequency was calculated as the number of samples in which spores of a particular morphotype occurred divided by the total number of samples and expressed as a percentage.

Species richness (*S*), Simpson's diversity index (*D*), Shannon–Wiener diversity index (*H*′) and the evenness index (*J*′) were calculated at the plot level. For three of the plots where the soil rhizosphere of two (two plots) or three species (one plot) was collected (Fig. 1b), the biodiversity indices were calculated separately for each host plant (n=34) using PAST 2.17 (Hammer et al. 2001).

Potential relationships among soil variables were analysed at plot level, considering host plant species separately (n=34) using Pearson's correlation. Bonferroni correction was employed for controlling experiment-wise error rates for multiple independent tests. A non-parametric Kruskal–Wallis test, combined with the Mann–Whitney *U* test with Bonferroni correction (p<0.05), was used at the plot level to determine differences in the total number of spores (TS) and diversity indices among the different host plants (*A. micrantha*, *E. grabriflora*, *Z. racemosa*) and topography (i.e. *baixio*, slope, plateau). Statistical testing was carried out using SYSTAT 10.0 (SYSTAT Inc., USA).

The relationship between soil variables and host species, and AMF relative spore abundance was analysed using redundancy analysis (RDA). Log-transformed data on the relative abundance of AMF spores and environmental variables at plot level were used to carry out the analysis. RDA was conducted using the vegan package in R 2.15.1 (Oksanen et al. 2013) to assess the influence of environmental variables and host identity on the composition and abundance of AMF communities.

Only environmental variables which significantly contributed (as assessed by the step function and by permutation tests) and resulted in the lowest Akaike information criterion value were included in the final model of the constraints.

Results

Fungal community composition and diversity

The density of spores ranged from 1.5 to 9.4 spores per gram of dry soil; 80.9 % (i.e. 23,883) of the total number of AMF spores detected in the soil rhizosphere of *A. micrantha* (18 individuals), *E. grabriflora* (48 individuals) and *Z. racemosa* (36 individuals; Table 1) were not damaged and therefore identifiable. The spores belonged to 41 AMF spore morphotypes, of which 39 were identified to species, one to genus and one remained unidentified. The AMF community was dominated by taxa belonging to the families Glomeraceae (15 taxa), Acaulosporaceae (seven taxa) and Gigasporaceae (six taxa). *Glomus* was the genus with the highest number of detected taxa (11), followed by *Acaulospora* (seven taxa) and *Claroideoglomus* and *Scutellospora* (four taxa). Species belonging to the genera *Glomus* and *Acaulospora* represented 44 % of the total species. Overall, 76 % of the identified AMF taxa were common to the rhizosphere of all host plants, whilst 15 % occurred exclusively in the rhizosphere of a single host species (Table 1).

The highest number of spores belonged to *Claroideoglomus etunicatum*, *Glomus fuegianum* and *Glomus macrocarpum*, whose frequencies in some cases reached 100 %.

Most of the spores were isolated as single spores, and only a few taxa appeared both as isolated spores and sporocarps. *Diversispora versiformis* had an average of 10 spores per sporocarp, *G. fuegianum* 12, *G. macrocarpum* 22, *Sclerocystis rubiformis* 6.5 and *Sclerocystis taiwanensis* 60. The species accumulation curves showed that whilst the number of fungal taxa associated with *E. grabriflora* and *Z. racemosa* nearly levelled off, a larger number of soil samples would have probably shown a higher number of fungal taxa in the rhizosphere of *A. micrantha*, indicating insufficient sampling (Fig. 2).

Topography and host identity had significant effects on species richness (*S*), total number of spores (*TS*), Simpson's diversity index (*D*) and Shannon–Wiener diversity index (*H*′), whilst the evenness index (*J*′) was affected exclusively by host identity (Table 2). *S* and *H*′ were significantly higher in the rhizosphere of *Z. racemosa* that in the other two hosts, whilst TS was higher in the rhizosphere of both *Z. racemosa* and *A. micrantha* (Table 3). *D* was higher in the rhizosphere

Table 1 Total number of spores (*TS*), relative frequency (*F*) and relative abundance (*A*) of arbuscular mycorrhizal fungal spores detected in the soil rhizosphere of three woody leguminous species in the Adolpho Ducke Forest Reserve: *A. micrantha*, *E. grabriflora* and *Z. racemosa*

AMF taxa	*A. micrantha*			*E. grabriflora*			*Z. racemosa*		
	TS	*F* (%)	*A* (%)	TS	*F* (%)	*A* (%)	TS	*F* (%)	*A* (%)
Acaulosporaceae									
Acaulospora aff. *brasiliensis* (Goto, Maia & Oehl) Walker, Krueger & Schüßler	0	0	0	24	8.70	0.31	1	2.86	0.01
Acaulospora colombiana (Spain & Schenck) Kaonongbua, Morton & Bever	2	5.88	0.03	12	15.22	0.15	13	14.29	0.13
Acaulospora foveata Trappe & Janos	1	5.88	0.02	0	0	0	0	0	0
Acaulospora mellea Spain & Schenck	7	17.65	0.12	60	36.96	0.77	38	40	0.38
Acaulospora morrowiae Spain & Schenck	23	29.41	0.38	45	10.87	0.58	44	40	0.44
Acaulospora rehmii Sieverding & Toro	7	11.76	0.12	126	45.65	1.61	60	51.43	0.60
Acaulospora aff. *scrobiculata* Trappe	0	0	0	0	0	0	2	2.86	0.02
Ambisporaceae									
Ambispora appendicula (Spain, Sieverding & Schenck) Walker	2	5.88	0.03	0	0	0	0	0	0
Ambispora aff. *leptoticha* (Schenck & Smith) Walker, Vestberg & Schüßler	1	5.88	0.02	10	17.39	0.13	30	34.29	0.30
Archaeosporaceae									
Archaeospora trappei (Ames & Linderman) Morton & Redecker	18	41.18	0.30	302	73.91	3.87	116	74.29	1.15
Claroideoglomeraceae									
Claroideoglomus claroideum (Schenck & Smith) Walker & Schüßler	297	82.35	4.94	283	60.87	3.63	282	74.29	2.80
Claroideoglomus drummondii (Błaszkowski & Renker) Walker & Schüßler	3	5.88	0.05	63	15.22	0.81	21	11.43	0.21
Claroideoglomus etunicatum (Becker & Gerdemann) Walker & Schüßler	642	94.12	10.68	668	80.43	8.56	674	100	6.69
Claroideoglomus luteum (Ken, Stutz & Morton) Walker & Schüßler	0	0	0	0	0	0	2	2.86	0.02
Diversisporaceae									
Diversispora aff. *eburnea* (Ken, Stutz & Morton) Walker & Schüßler	67	47.06	1.11	203	52.17	2.60	343	85.71	3.41
Diversispora aff. *pustulata* (Koske, Friese, Walker & Dalpé) Oehl, Silva & Sieverding	61	47.06	1.02	93	28.26	1.19	247	88.57	2.45
Diversispora versiformis (Karsten) Oehl, Silva & Sieverding	570	94.12	9.49	295	76.09	3.78	783	97.14	7.78
Entrophosporaceae									
Entrophospora sp. (*baltica*-like)	91	58.82	1.51	174	47.83	2.23	279	97.14	2.77
Gigasporaceae									
Gigaspora rosea Nicolson & Schenck	2	5.88	0.03	9	10.87	0.12	8	14.29	0.08
Racocetra castanea (Walker) Oehl, Souza & Sieverding	168	82.35	2.80	289	84.78	3.70	336	94.29	3.34
Scutellospora arenicola Koske & Halvorson	7	17.65	0.12	146	76.09	1.87	9	14.29	0.09
Scutellospora calospora Nicolson & Gerdemann	0	0	0	1	2.17	0.01	3	8.57	0.03
Scutellospora cerradensis Spain & Miranda	0	0	0	3	2.17	0.04	0	0	0
Scutellospora dipurpurescens Morton & Koske	9	23.53	0.15	50	34.78	0.64	96	80	0.95
Glomeraceae									
Funneliformis aff. *badium* (Oehl, Redecker & Sieverding) Walker & Schüßler	749	94.12	12.46	475	82.61	6.09	840	97.14	8.34
Funneliformis geosporum (Nicolson & Gerdemann) Walker & Schüßler	39	52.94	0.65	183	73.91	2.34	176	74.29	1.75
Glomus aff. *atrouva* McGee & Pattinson	1	5.88	0.02	7	8.70	0.09	40	31.43	0.40
Glomus aff. *australe* (Berkeley) Berch	83	76.47	1.38	170	69.57	2.18	134	68.57	1.33
Glomus aff. *brohultii* Sieverding & Herrera	307	76.47	5.11	887	91.30	11.36	629	85.71	6.25
Glomus diaphanum Morton & Walker	165	76.47	2.75	7	4.35	0.09	0	0	0
Glomus fuegianum (Spegazzini) Trappe & Gerdemann	743	100	12.36	1085	97.83	13.90	1083	100	10.76

Table 1 (continued)

AMF taxa	*A. micrantha*			*E. grabriflora*			*Z. racemosa*		
	TS	*F* (%)	*A* (%)	TS	*F* (%)	*A* (%)	TS	*F* (%)	*A* (%)
Glomus heterosporum Smith & Schenk	237	52.94	3.94	268	63.04	3.43	464	91.43	4.61
Glomus macrocarpum Tulasne & Tulasne	1235	100	20.55	1092	89.13	13.99	1805	100	17.93
Glomus microcarpum Tulasne & Tulasne	4	11.76	0.07	0	0	0	0	0	0
Glomus minutum Błaszkowski, Tadych & Madej	76	35.29	1.26	41	34.78	0.53	134	85.71	1.33
Glomus aff. *spinosum* Hu	170	82.35	2.83	202	71.74	2.59	99	60	0.98
Glomus aff. *tenebrosum* (Thaxter) Berch	166	82.35	2.76	358	73.91	4.59	403	82.86	4.00
Sclerocystis rubiformis Gerdemann & Trappe	0	0	0	32	21.74	0.41	292	62.86	2.90
Sclerocystis taiwanensis Wu & Chen	5	11.76	0.08	13	10.87	0.17	497	91.43	4.94
Pacisporaceae									
Pacispora robigina Sieverding & Oehl	42	47.06	0.70	60	39.13	0.77	36	25.71	0.36
Not identified species	9	11.76	0.15	70	50	0.90	49	37.14	0.49
Total no. of spores	6,009			7,806			10,068		
Total no. of species	35			36			36		

of *A. micrantha* than *Z. racemosa*, whilst *J′* was significantly lower in the rhizosphere of *A. micrantha* than *Z. racemosa* (Table 3). *S* and TS were significantly higher on plateaux than *baixios*, whilst *D* was higher on *baixios* than plateaux and *H′* was higher on slopes than *baixios* (Table 3).

Environmental predictors and fungal communities

Topographic position (altitude) correlated positively with Mn^{2+}, K^{+}, Al^{3+}, Fe and Zn^{+} concentrations and with clay and silt contents. It correlated negatively with pH and sand content (Table 4).

AFM spore community abundance was attributable to both soil conditions and host identity. The variation of the AMF community composition was significantly related to two of three measured environmental variables—soil clay and sand contents and soil moisture (Fig. 3)—and to two host species—*A. micrantha* and *Z. racemosa*—that together explained 44.84 % of the total inertia (RDA: axis 1, eigenvalue=3.643; axis 2, eigenvalue=1.813). The abundance of spores of AMF species such as *Diversispora* aff. *eburnea*, *D.* aff. *pustulata*, *D. versiformis*, *Entrophospora* sp. (*baltica*-like) and *G. macrocarpum*, was higher on clayey soils. The abundance of spores of *D.* aff. *pustulata* and *Entrophospora* sp. (*baltica*-like) was also positively correlated with soil moisture, whilst that of *Glomus* aff. *spinosum* was negatively correlated with soil moisture. The abundance of spores of species such as *Archaeospora trappei*, *Funneliformis geosporum*, *Glomus* aff. *brohultii*, *G. fuegianum* and *Scutellospora arenicola* was higher on sandy soils. *Glomus diaphanum* spore abundance was positively correlated with *A. micrantha*, whilst the spore abundance of species such as *D.* aff. *eburnea*, *S. rubiformis* and *S. taiwanensis* was closely related with *Z. racemosa*.

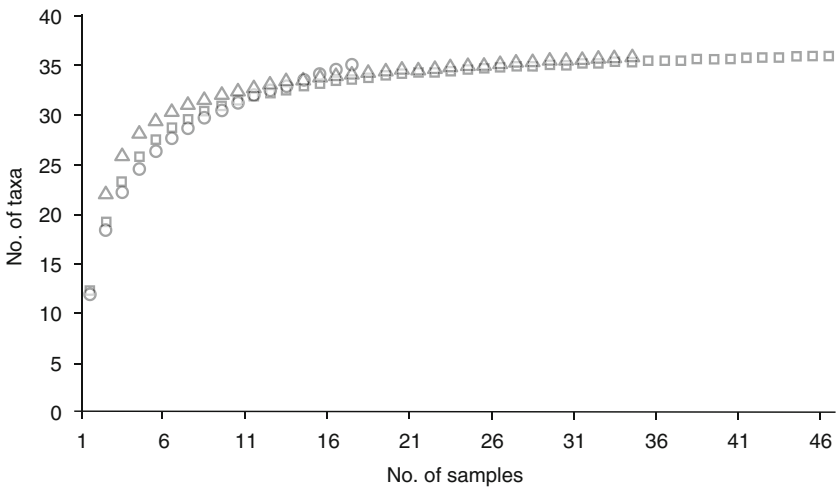

Fig. 2 Coleman rarefaction curves for arbuscular mycorrhizal fungal taxa associated with the soil rhizosphere of three leguminous species (*circles*, *A. micrantha*; *squares*, *E. grabriflora*; *triangles*, *Z. racemosa*) occurring along a topographic gradient of a primary terra firme tropical forest within the Adolfo Ducke Forest Reserve (Manaus, Amazonas)

Table 2 Results of the analysis of parameter estimates from the Kruskal–Wallis test on the effects of host identity and topography on the species richness (*S*), total number of spores (*TS*), Simpson's diversity index (*D*), Shannon–Wiener diversity index (*H′*) and evenness index (*J′*) of arbuscular mycorrhizal fungal spores detected in the soil rhizosphere of three woody leguminous species along a pedo-hydrological gradient in the Adolpho Ducke Forest Reserve

	S		TS		*D*		*H′*		*J′*	
	Hc	*p*	Hc	*p*	Hc	*p*	Hc	*p*	Hc	*p*
Host	13.47	**	15.44	***	12.12	**	14.65	***	7.25	*
Topography	13.62	**	12.80	**	8.30	*	9.04	*	3.52	ns

Hc corresponds to *H* statistic corrected for ties

*$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$

Discussion

The AMF spore community present in the rhizosphere soil of three leguminous woody species (*A. micrantha*, *E. grabriflora*, *Z. racemosa*) has been evaluated along a topo–pedo–hydro gradient in a terra firme tropical forest. The total number of spore morphotypes detected (41) in the present study was intermediate between those found in the Amazon region by Stürmer and Siqueira (2011, 61 taxa), Leal et al. (2009, 24 taxa) and Peña-Venegas et al. (2007, 18 taxa), although the number of AMF taxa is certainly underestimated in this study due to the restricted temporal sampling. The fungal community was characterised by the dominance of species belonging to the genera *Glomus* (27 %) and *Acaulospora* (17 %). This pattern confirmed data observed in the Amazon region (Martin et al. 2001; Caproni et al. 2003; Peña-Venegas et al. 2007; Stürmer and Siqueira 2011) and is similar to that of tropical systems worldwide (Musoko et al. 1994; Guadarrama and Álvarez-Sánchez 1999; Picone 2000; Husband et al. 2002; Zhao et al. 2003; Mangan et al. 2004; Guadarrama-Chávez et al. 2007). Spore density in the rhizosphere soil of the sampled species ranged from 1.5 to 9.4 per 1 g of soil. Comparable values were found in native tree legumes in Uruguay (2.8–16.2 spores per gram; Frioni et al. 1999) and in the tropical rainforest of Xishuangbanna in China (0.6–19.1 spores per gram; Zhao et al. 2003), whilst higher spore densities occurred in the rhizosphere of two leguminous species of a primary forest in the French Guiana (50–154 spores per gram; Martin et al. 2001).

The ordination analysis showed that the variability within AMF communities in the present study was largely associated with shifts in the relative abundance of spores rather than changes in species composition. The spore abundance of AMF taxa differed along the topographic gradient depending on whether soils were collected from plateaux or *baixios*. Specifically, some taxa (e.g. *D.* aff. *eburnea*, *D.* aff. *pustulata*, *D. versiformis*, *Entrophospora* sp. (*baltica*-like), *G. macrocarpum*) were significantly more abundant in clayey soil on plateaux and were also positively correlated with soil moisture (e.g. *D.* aff. *pustulata* and *Entrophospora* sp. (*baltica*-like)), whilst the abundance of other taxa (e.g. *A. trappei*, *F. geosporum*, *G.* aff. *brohultii*, *G. fuegianum* and *S. arenicola*) was higher on the sandier soils of *baixios*. Differences in the AMF community composition and abundance between clay and sandy soils were previously found associated with maize roots from sand and clay soils in a farming region of southwest Zimbabwe, with Gigasporaceae dominating in sandy soil and Glomeraceae dominating in clay soil (Lekberg et al. 2007). In the present study, the

Table 3 Species richness (*S*), total number of spores (*TS*), Simpson's diversity index (*D*), Shannon–Wiener diversity index (*H′*) and evenness index (*J′*) of arbuscular mycorrhizal fungal spores detected in the soil rhizosphere of three woody leguminous species (*A. micrantha*, *E. grabriflora*, *Z. racemosa*) along a pedo-hydrological gradient (*baixio*, slope, plateau) in the Adolpho Ducke Forest Reserve

		S	TS	*D*	*H′*	*J′*
Host	*A. micrantha*	22.8 (±1)a	360.433 (±34)a	0.118 (±0.005)a	2.441 (±0.034)a	0.784 (±0.012)a
	E. grabriflora	23.6 (±0.8)a	173.969 (±17)b	0.109 (±0.008)ab	2.588 (±0.055)a	0.820 (±0.013)ab
	Z. racemosa	27.4 (±0.4)b	286.633 (±24)a	0.086 (±0.003)b	2.770 (±0.021)b	0.837 (±0.006)b
Topography		22.5 (±0)a	174.536 (±21)a	0.117 (±0.008)a	2.510 (±0.052)a	0.808 (±0.014)
		25.3 (±1)ab	270.378 (±35)ab	0.092 (±0.007)ab	2.721 (±0.067)b	0.843 (±0.012)
		27 (±0.6)b	318.982 (±22)b	0.093 (±0.004)b	2.697 (±0.040)ab	0.815 (±0.009)

Values with lowercase letters indicate statistically significant differences between host species and topography as determined by Mann–Whitney *U* test, followed by Bonferroni correction ($p<0.05$)

Table 4 Pearson's correlations between environmental variables recorded at the Adolpho Ducke Forest Reserve (n=34)

	Altitude	pH	Ca^{2+}	Mg^{2+}	K^{+}	P	Al^{3+}	Fe	Zn^{+}	Mn^{2+}	Moisture (%)	Clay (%)	Silt (%)	Sand (%)
Altitude	1.000													
pH	−0.802***	1.000												
Ca^{2+}	0.220	−0.286	1.000											
Mg^{2+}	0.653**	−0.617**	0.751***	1.000										
K^{+}	0.786***	−0.713***	0.595	0.909***	1.000									
P	−0.055	−0.172	0.520	0.344	0.349	1.000								
Al^{3+}	0.928***	−0.882***	0.324	0.709***	0.820***	0.091	1.000							
Fe	0.783***	−0.734***	0.058	0.405	0.508	−0.092	0.836***	1.000						
Zn^{+}	0.718***	−0.702**	0.415	0.700**	0.767***	0.234	0.780***	0.504	1.000					
Mn^{2+}	0.724***	−0.717***	0.333	0.652**	0.722***	0.272	0.791***	0.609*	0.697**	1.000				
Moisture (%)	0.457	−0.309*	0.362	0.466	0.400	0.022	0.386	0.287	0.304	0.443	1.000			
Clay (%)	0.978***	−0.784***	0.270	0.671**	0.793***	−0.050	0.912***	0.773***	0.686**	0.698**	0.478	1.000		
Silt (%)	0.883***	−0.696**	0.378	0.627*	0.724***	0.076	0.847***	0.704**	0.655**	0.659**	0.496	0.912***	1.000	
Sand (%)	−0.977***	0.781***	−0.283	−0.672**	−0.793***	0.038	−0.913***	−0.773***	−0.688**	−0.700**	−0.483	−0.999***	−0.928***	1.000

*p<0.05; **p<0.01; ***p<0.001

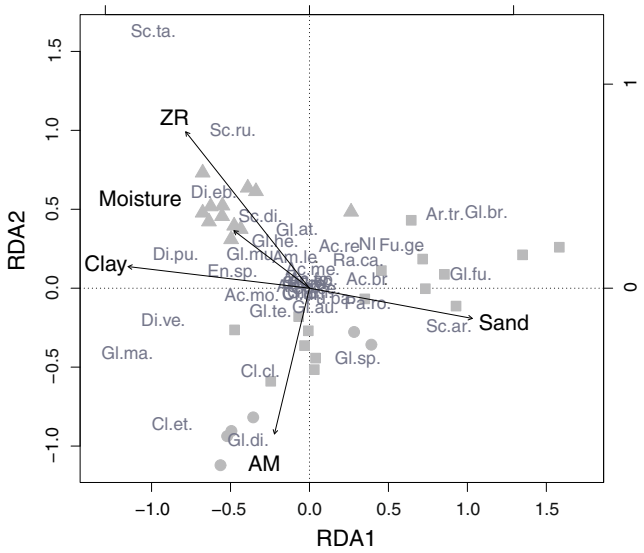

Fig. 3 Results of a RDA made on the relative abundance data of arbuscular mycorrhizal fungal taxa associated with the rhizosphere of three leguminous species occurring along a topographic gradient of a primary terra firme tropical forest within the Adolfo Ducke Forest Reserve (Manaus, Amazonas). *Each symbol* represents a 40×250-m plot (*circles*, *A. micrantha*; *squares*, *E. grabriflora*; *triangles*, *Z. racemosa*). Axes 1 and 2 explain 44.84 % of the variance of the species data. *Ac.br. Acaulospora* aff. *brasiliensis*, *Ac.co. Acaulospora colombiana*, *Ac.fo. Acaulospora foveata*, *Ac.me. Acaulospora mellea*, *Ac.mo. Acaulospora morrowiae*, *Ac.re. Acaulospora rehmii*, *Ac.sc. Acaulospora* aff. *scrobiculata*, *Am.ap. Ambispora appendicula*, *Am.le. Ambispora* aff. *leptoticha*, *Ar.tr. Archaeospora trappei*, *Cl.cl. Claroideoglomus claroideum*, *Cl.dr. Claroideoglomus drummondii*, *Cl.et. Claroideoglomus etunicatum*, *Cl.lu. Claroideoglomus luteum*, *Di.eb. Diversispora* aff. *eburnea*, *Di.pu. Diversispora* aff. *pustulata*, *Di.ve. Diversispora versiformis*, *En.*sp. *Entrophospora* sp. (*baltica*-like), *Fu.ba. Funneliformis* aff. *badium*, *Fu.ge. Funneliformis geosporum*, *Gl.at. Glomus* aff. *atrouva*, *Gl.au. Glomus* aff. *australe*, *Gl.br. Glomus* aff. *brohultii*, *Gl.di. Glomus diaphanum*, *Gl.fu. Glomus fuegianum*, *Gl.he. Glomus heterosporum*, *Gl.ma. Glomus macrocarpum*, *Gl.mi. Glomus microcarpum*, *Gl.mu. Glomus minutum*, *Gl.sp. Glomus* aff. *spinosum*, *Gl.te. Glomus* aff. *tenebrosum*, *Gi.ro. Gigaspora rosea*, *Pa.ro. Pacispora robigina*, *Ra.ca. Racocetra castanea*, *Sc.ru. Sclerocystis rubiformis*, *Sc.ta. Sclerocystis taiwanensis*, *Sc.ar. Scutellospora arenicola*, *Sc.ca. Scutellospora calospora*, *Sc.ce. Scutellospora cerradensis*, *Sc.di. Scutellospora dipurpurescens*, NI non-identified species. *Clay* soil clay content, *Sand* soil sand content, *Moisture* soil moisture, *AM A. micrantha*, *ZR Z. racemosa*

major number of species found in sandy soil belonged to Glomeraceae, whilst Diversisporaceae dominated in clay soils that were also characterised by higher species richness and total number of spores than *baixios*. Low fungal propagule densities were found to be associated with sandy soils by Sieverding (1991) and Souza et al. (2003). The authors linked low spore densities with stress conditions that plant host endure in sandy soils and the vulnerability of these soils to disturbance that facilitates the attack of propagules by parasites and increases their susceptibility to dispersal agents. At the study site, most *baixios* areas experience periodic flooding during periods of high precipitation. Furthermore, soil samples were collected during the transition between the rainy and dry seasons, and this could partly explain the lower number of AMF species and spore densities in these areas.

Soil texture strongly influences soil drainage and nutrient availability and retention, particularly in highly weathered soils (Silver et al. 2000). In the tropics, under natural conditions, clayey soils tend to have higher cation exchange capacity and higher litter decomposition rates than sandy soils (Uehara 1995). The nutrient concentrations varied in the study area along the pedo-hydrological gradient, with plateaux characterised by higher levels of Mg^{2+}, K^{+}, Fe, Zn^{+} and Mn^{2+} than *baixios*. In a previous study conducted in the same area, it was found that total nitrogen in the topsoil was also significantly higher in plateaux than *baixios* (Luizão et al. 2004). Since the optimal amount of resources differs among fungal species (Murray et al. 2010), the heterogeneity of soil nutrient availability in the study area could explain the differences in spore abundance between plateaux and *baixios*, but interpretation is difficult as the topography/hydrology and soil nutrient status are linked.

AMF species could also be indirectly affected through the host plant which, depending on nutrient availability, could deliver different levels of C to fungal associates (Murray et al. 2010). Host plant identity can therefore determine the composition and relative abundance of AMF species by influencing sporulation rates, growth (Bever et al. 2001) and survival of different mycorrhizal species (Bever et al. 1996). Whilst the identity of AMF species in host plant roots was not verified in the present study, tree host identity affected AMF spore community abundance and diversity in rhizosphere soils. Species like *G. diaphanum* were found almost exclusively in the rhizosphere of *A. micrantha*, whilst the spore abundance of species like *D.* aff. *eburnea*, *S. rubiformis* and *S. taiwanensis* was highly related to *Z. racemosa*, which was characterised by higher species richness and evenness than *E. grabriflora* and *A. micrantha*. These results are in agreement with those of Musoko et al. (1994) and Lovelock et al. (2003) who found that tropical host species offered differential environments for AMF sporulation. Nevertheless, whilst the degree of specificity in mycorrhizal associations could result from a direct response of the fungal symbiont to the host or from a response to microenvironmental conditions associated with the host species (Fitter 2005), common AMF species are widely distributed in plant communities and all plants recruited into the forest are likely to be exposed to the dominant sporulating AMF species (Lovelock et al. 2003).

Several limitations of the present study have to be considered. Firstly, the characterization of the AMF community was based exclusively on field-collected spores whilst molecular analysis of field-collected roots could have provided

the full spectrum of AMF species (Vandenkoornhuyse et al. 2002a). In addition, the number of spores for some AMF species is not always correlated with the proportion of root length colonized by the fungus (Merryweather and Fitter 1998a, b). Some authors found, however, a large overlap of the AMF communities in roots and spores, with a wider diversity in the spore fraction, and suggested that roots only recruit a fraction of the AMF taxa pool present as spores in soils (Johnson et al. 2003; Hempel et al. 2007). Therefore, spore community assessment should allow a reliable evaluation of the differences induced by biotic and abiotic factors on the AMF communities (Lovelock and Ewel 2005).

Secondly, the occurrence of AMF was assessed only once, during the transition between the rainy and dry seasons. AMF can differ in their seasonality (Bever et al. 2001), with sporulation rates that vary throughout the growing season and that are highly species-dependent (Smith and Read 2008). Therefore, not all species of the AMF community in the study area had possibly sporulated at the time of sampling. Moreover, whilst little is known about the longevity of AMF propagules, differences in spore morphology could have cause differences in the persistence of spores in the soil (Carrenho et al. 2001). However, although information on spore abundance obtained using exclusively the morphological characterization of field-collected spores at one sampling date has to be interpreted with caution (Murray et al. 2010), relative differences among spore composition and abundance provide a useful tool for investigating the ecology of AMF communities (Lovelock et al. 2003).

In conclusion, the findings of the present study corroborate the importance of niche partitioning, in particular soil texture and moisture content, in shaping AMF communities. Shifts in the relative abundance of spores rather than changes in species composition were observed along a pedo-hydrological gradient. Whilst plant host identity explained, together with soil texture and moisture, the variation in AMF relative abundance, species composition was not affected by either abiotic and biotic variables, confirming that common AMF species are widely distributed in plant communities and all plants recruited into the forest are likely to be exposed to the dominant sporulating AMF species.

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