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# How do seasonality, substrate, and management history influence macrofungal fruiting assemblages in a central Amazonian Forest?

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## ABSTRACT

Worldwide, fungal richness peaks in tropical forest biomes where they are the primary drivers of decomposition. Understanding how environmental and anthropogenic factors influence tropical macrofungal fruiting patterns should provide insight as to how, for example, climate change and deforestation may impact their long-term demographic stability and evolutionary potential. However, in Amazonia no studies have yet to disentangle the effects of substrate, seasonality and forest history on phenology. Here, we quantitate spatial and temporal variation in community structure of fruiting macrofungi in relation to these factors at a long-term forest management research site in central Amazonia: the Biomass and Nutrients of Tropical Rain Forest (BIONTE's). Basidiome surveys of four substrate classes (leaves, soil, branches and trunks) were conducted along 250 $m^2$ transects in primary and secondary (managed) forests, between 2012–13. From the 669 basidiomes collected, 290 taxa were identified of which 44 percent were restricted to primary and 36 percent to secondary forests. Although species-accumulation curves did not asymptote, rarefaction analyses and Fisher's alpha indicate contrasting differences in richness among forests in relation to substrate type. For example, leaf litter basidiome richness was higher in secondary forests, whereas the contrary was observed for soil communities, suggesting that variation in fruiting patterns in relation to disturbance is substrate-dependent possibly due to differences in necromass quality and/or understory micro-climates. Furthermore, secondary forests harbored significantly lower basidiome richness and abundance in dry months, suggesting synergistic impacts of seasonality and management history on fruiting regimes.

Abstract in Portuguese is available with online material.

*Key words*: Agaricales; Amazon; Brazil; forest management; fungi; rain forest; rarefaction.

FUNGI ARE IMPORTANT COMPONENTS OF TROPICAL FORESTS DUE TO THEIR FUNDAMENTAL role in nutrient cycling dynamics and primary production (Lodge *et al.* 1996). However, their metabolic activity and fruiting phenologies are affected by changes in temperature and humidity (Lodge & Cantrell 1995). Indeed, warming trends in temperate regions have repeatedly been correlated with shifting fruiting times in macrofungi communities (Gange *et al.* 2007, Kauserud *et al.* 2012). Nonetheless, little is known about how climate change may affect tropical fungal fruiting phenology. In Amazonia, global climate models predict that annual precipitation will decline across large sections of this biome during the next decade (Cai *et al.* 2015, LI *et al.* 2011, Lewis *et al.* 2011, Harris *et al.* 2008). In such a scenario, the capacity of fungi to recycle vegetal necromass may be compromised since the synergistic effects of drying trends, anthropogenic disturbance and changes in plant community structure (Peay *et al.* 2013) may imply unpredictable consequences among these aspects of Amazonian biodiversity.

Forest history is an additional complicating factor potentially altering the dynamics of plant-fungal associations in tropical biomes. Relatively well documented in Amazonia, for example, are the impacts of forest fragmentation on tree community structure and the subsequent cascade of effects on other groups (Laurance *et al.* 2011). The accompanying changes in aboveground biomass, soil nutrient retention and tree regeneration capacity following deforestation are also well studied (Feldpausch *et al.* 2004, Nascimento & Laurence 2004, Bentos *et al.* 2013). Indeed, experimental studies of leaf litter characteristics conclude that differences in decomposition rates among primary and secondary forests are principally due to diverging tree composition and correlated chemical and physical properties of their leaves which form the organic layer (Luizão 1989, Vasconcelos & Laurence 2005, Barlow *et al.* 2007). However, no studies have yet to provide complementary evidence on changes in Amazonian fungal communities, and, as a consequence, leaving a fundamental piece of this puzzle missing.

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Extra-Amazonian studies of forest management practice impacts on macrofungal communities have been limited to specific groups (Chaverri & Vílchez 2006), focal host species (Tsui *et al.* 1998) or comparisons among heavily modified landscapes (*e.g.*, monocultural tree plantations) (Paz *et al.* 2015). Nonetheless, the general consensus is that fungal diversity is inversely related to time since disturbance and positively related to that of the diversity of their associated plant communities. For example, in an eastern Costa Rican rain forest, Chaverri and Vílchez (2006) showed that hypocrealean microfungi, a guild of ascomycetes with demonstrably high host specificity on living plants, were less diverse in more mature forests. In subtropical Brazil, exotic tree plantations of *Pinus* and *Eucalyptus* forest showed less similar macrofungal composition to native *Araucaria angustifolia* forests than did monoculture stands of the same native species, suggesting that the conversion into exotic tree plantations reduces the number of macrofungal taxa due to changes in substrate type and quality (Paz *et al.* 2015).

Although basidiome surveys only provide a profile of the fruiting component of macrofungi assemblages, they are effective in identifying factors which contribute to phenological changes of macrofungal communities in relation to environmental, historical, or climatological factors (Lodge & Cantrell 1995, Lodge *et al.* 2004, O'Dell *et al.* 2004, Gange *et al.* 2007). Such surveys, however, do not necessarily capture the entire mycelial community of a given area. For example, in a temperate forest stand in Canada, basidiome sampling resulted in a different species assemblage than that recovered from genetic screening of soils, indicating that no single sampling method can fully unravel soil fungi communities in a temperate forest (Porter *et al.*2008). Nonetheless, basidiome production indicates mycelia activity and basidiome surveys at least point to a subset of taxa sufficiently established to engage in sexual reproduction.

Another impediment to fungal community studies in tropical regions is the difficulty of species identification. Phenotypic convergence, plasticity, and a surplus of undescribed taxa from understudied regions all contribute to this challenge (Braga-Neto *et al.* 2008, Piepenbring *et al.* 2012). Tropical regions, such as Amazonia, which harbor the greatest diversity of most major fungal groups (Tedersoo *et al.* 2014) are woefully understudied, creating a combination of taxonomic challenges and, consequently makes formidable barriers to advancing into macrofungi community ecology studies. Investment in intensive, long-term monitoring programs with taxonomic studies and genetic screening is ideal for assuring a comprehensive registry of mycelial communities in a given area (Aime & Brearley 2012).

In light of these challenges, the aim of this study was to investigate how seasonality and forest history influence basidiome community structure. We conducted a 2-year basidiome survey of Agaricales in primary and selectively managed forests as they occurred on four substrate types (trunks, branches, soil, and leaf litter) to address the following hypotheses. First, due to the fact that agaric fungi accumulate more biomass in wet when compared to dry cycles (Lodge 1993), we predict basidiome richness to be more variable among seasons than among forest types. Furthermore, we predict contrasting guild-dependent responses as suggested by the fact that the quality of certain substrates, such as soil, are negatively impacted (Hartmann *et al.* 2014) whereas that of others, such as rotting trunks, branches, and leaf litter are positively impacted by forest management (Mesquita *et al.* 1997, Nascimento & Laurence 2004). Considering that disturbed forests and edge habitats are characterized by greater necromass production (Nascimento & Laurence 2004), key substrates for macrofungal growth, we hypothesize higher density and richness of these guilds in managed forest plots.

## METHODS

Study site.—The study area is located at the Experimental Station for Forest Management (ZF-2) operated by Brazil's National Institute for Amazonian Research (INPA) *ca* 80 km north of Manaus, AM, Brazil (02°37′ and 02°38′S; 60°09′ and 60°11′W) (Fig. S1). The vegetation is upland Amazonian rain forest with high floristic heterogeneity. The soils are yellow latosol, with high clay content, acid with high quantities of aluminum and low capacity of cation exchange (Chauvel 1982). The climate is warm with high precipitation during the year, the driest month typically occurring in August (*ca* 100 mm) and the rainiest months from February to June (>290 mm) (Ferreira *et al.* 2006).

In the 1980s, INPA developed forest management experiments with the goal of researching methods of sustainable wood production. In 1987, the project 'BIONTE'—The Biomass and Nutrients of Tropical Rain Forest, performed experiments with selective wood extraction to understand the ecological effects of this process (Ferreira *et al.* 2006). This study used an experimental design comprised of two blocks of BIONTE's Project at INPA's Experimental Forest Management Station each with six plots at 200 × 200 m (Higuchi *et al.* 1997).

The collection sites present the same type of soil characteristics and altitude (Luizão *et al.* 2001), the difference between primary and secondary forest corresponds to differences in tree age and composition. The secondary forest underwent a clear-cut 27 years ago as part of the BIONTE experiment, and is primarily composed of Melastomataceae (*Miconia tomentosa* (Rich.) D. Don ex DC., *Bellucia dichotoma* Cogn., Urticaceae (*Cecropia* sp., *Pourouma* sp.) and Rubiaceae of which none exceed 15.2 cm dbh (diameter at breast height). The canopy is open, allowing the light to reach the forest floor, which results in more rapid desiccation of ground substrates especially during the dry season. On the other hand, the primary forest canopy tree composition consists of a wider range of families, including Lecythidaceae, Leguminosae, Moraceae, Myrtaceae, Sapotaceae, Lauraceae, and Burseraceae (Gaui 2013), thus contributing to substantially higher substrate heterogeneity. The understory, unlike secondary forests, is dominated by the palm *Astrocaryum sciophilum* (Miq.) Pulle.

Sampling design.—Sampling plots were established as 5 × 50 m transects, divided into 10 subplots (5 × 5 m):four band transects in primary forest (block I and II from the control plot of the Bionte's project); and four in nearby managed forests (Fig. S1)

totaling 40 subplots and eight transects. The fungi belonging to Agaricales were collected between May 2012 and September 2013 over 6 months during both years. Specifically, three consecutive months were collected during the height of the rainy (April–June), and dry (August–October) season resulting in a total of 12 inventories during the course of the study. To avoid temporal bias on basidiome detection, we visited in the same day one primary and one managed forest transect. Multiple basidiomes of the same species within each subplot or the same piece of substrate were counted as one occurrence. For each collection, substrate type was noted and divided into the following classes: rotting trunk (>10 cm diam.), branches (<10 cm diam.), leaves including petioles and soil (basidiomes collected directly on humus). No mushrooms were observed on living trees.

Taxonomic identification.—Basidiomes were described macroscopically in the field following Largent (1973) and Lodge *et al.*(2004), photographed, and subsequently dried using a food dehydrator and/or silicagel. Microscopic observations followed Largent *et al.* (1973) and specific literature according to the group. Specimens were separated into morphospecies and, when possible, identified to species. The literature used to identify specimens was mostly based on Singer (1964, 1976, 1986, 1989) as well as personal communication with specialists. Voucher specimens are deposited in the National Institute for Amazonian Research herbarium (INPA).

Data analysis.—To quantitate diversity we used Fisher's alpha index (Magurran 1988) partitioned by substrate type and season, using the R v. 3.1.3 (R Development Core Team 2015) and R packages 'vegan' (Oksanen *et al.* 2007). Individual-based species accumulation curves were generated by rarefaction and extrapolation using the iNEXT program (Hsieh *et al.* 2013, Chao *et al.* 2014). Rarefaction curves were based on a matrix of abundance data as the module estimates how many taxa would be expected at smaller sample sizes. Accumulation curves allow statistically confident comparisons of taxonomic richness among samples of different sizes effectively decoupling density bias from richness (Chao *et al.* 2014).

To test whether changes in abundance and species richness from wet to dry season was dependent on forest type (interaction of forest history/season), we performed a contingency table (Fisher's exact test) on the pooled data across forest history versus season.

Community composition was summarized by principal coordinates analysis (PCoA) based on the abundance of taxa in each transect and according to forest treatment and substrate. The Jaccard dissimilarity index corrected for undetected shared taxa (Chao *et al.* 2005) was used as the distance measure. Although the Jaccard dissimilarity index uses only presence-absence data, the method used here takes into account the abundance of taxa to correct for imperfect sampling (Chao *et al.* 2005). To further reduce the excess of rare taxa we also grouped species by genera to estimate fungal composition in relation to forest history and substrate.

Statistical tests comparing forest types and season, and measures of the Jaccard similarity index were performed in the R program (R Core Team 2015). The R function used to calculate the Jaccard similarity index between multiple sites using the method described in Chao *et al.* (2005) is provided as supporting information (Appendix S1), and online at https://dx.doi.org/10.6084/m9.figshare.3158995.v1. Fisher's exact test was employed to test for statistical differences in basidiome abundance and richness among seasons and forest histories.

## RESULTS

Basidiome richness and diversity in relation to substrate, season and forest type.—During the 2-year survey, we recorded 669 basidiomes classified into 290 taxa (Table S1 and examples of macrofungal diversity in Fig. 1) of which 129 (44%) were exclusive to primary forests, 103 (36%) solely in secondary forests, and 57 (20%) occur in both forest types. Basidiome richness (Fig. 2) varied among secondary and primary forests depending on substrate type. Although leaf litter fungi had higher basidiome richness in secondary forests (Fig. 2B), soil communities were richer in primary forests (Fig. 2C). However, no significant differences were observed among basidiome assemblies on rotting trunks and branches from the two forest types (Fig. 2A and D), or when data from all substrate types were combined (Fig. 2E). Most species found in trunks were rare, leading to broad confidence intervals in species accumulation curves and estimates of species richness, therefore, affecting our ability to detect differences in species richness between forest types for trunks. Despite the high number of rare species found in soil samples, and the broad confidence intervals for this group, the expected number of species was much lower in secondary forests than in primary forests.

Fisher's alpha corroborated with the richness values, as illustrated by the rarefaction curves, in all cases except for large necromass, where primary forests harbored slightly greater basidiome diversity. No overall differences in diversity were observed among secondary and primary plots (Table 1).

Sharp declines in basidiome abundance and species richness characterized all dry season samples (Fig. 2F). The decline in abundance and species richness in the dry season was disproportionately stronger in secondary when compared to primary forests ($P = 0.0005$ and 0.008; odds ratio = 3.05 and 2.78 for abundance and richness) suggesting a synergistic effect of seasonality and forest history. In primary forests, the number of species observed during the dry season was 16 percent of the number of species observed during the rainy season (29 vs. 177). In contrast, in secondary forests, only 6 percent of the species found during the rainy season (155) were also found during the dry season. Similarly, dry season basidiome abundances were 15 percent of that found in the wet season for primary forest and 5 percent for managed forests. A majority of the species restricted to one of the two forest types were only recorded during the wet season, and only eight taxa from primary and two from secondary forests were uniquely observed in the dry season.


FIGURE 1. Sample sites and macrofungal diversity and substrate. (A) and (B) Primary forest; (C) and (D) Secondary forest; (E) *Leucocoprinus brunneoluteus* on soil; (F) *Marasmius bellus* on leaf; (G) *Marasmius haematocephalus* on leaf; (H) *Mycena spinosissima* on branch; (I) *Marasmius phaeus* on trunk. Scale bars: E = 20; H = 10; F, G, I = 5 mm.

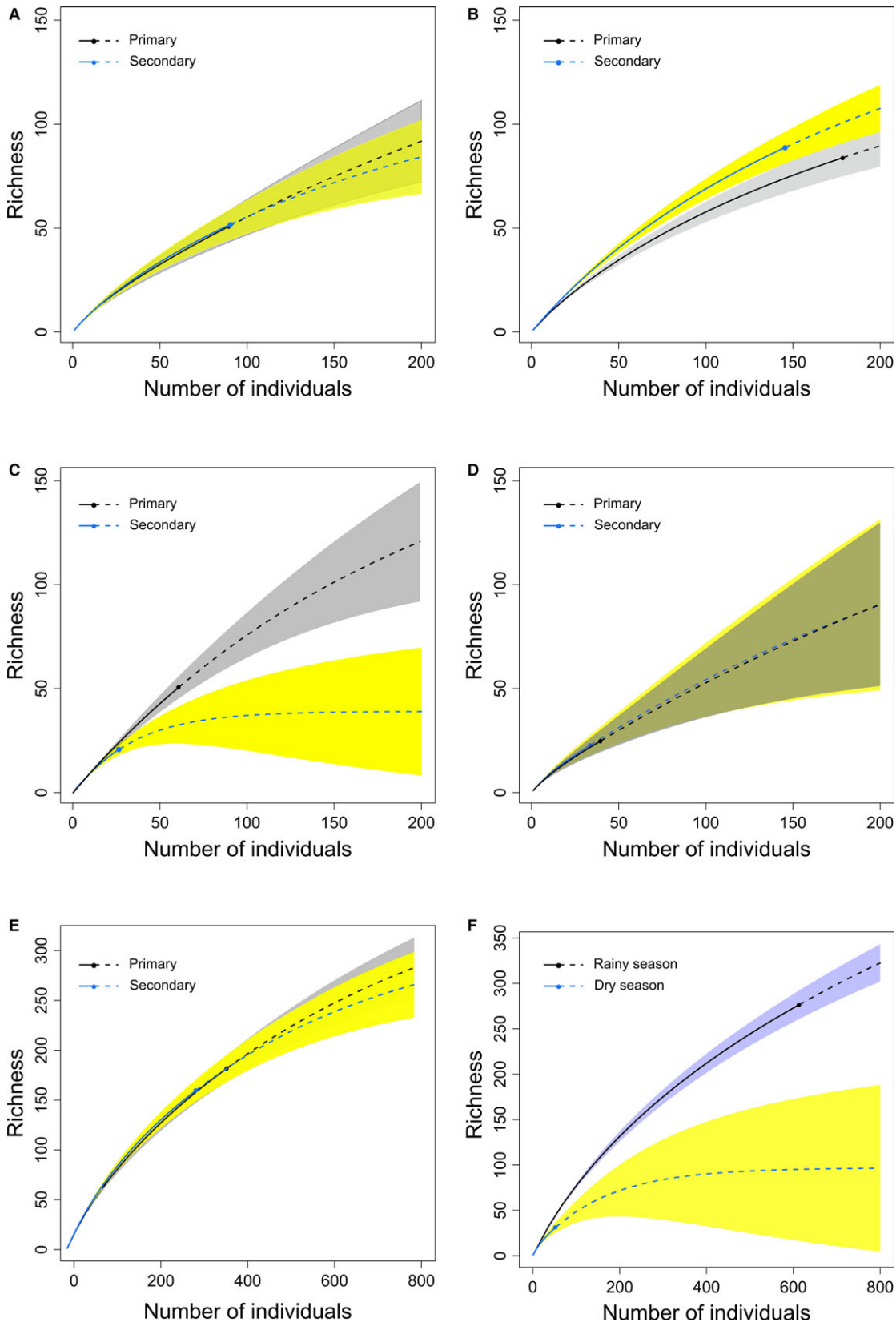


FIGURE 2. Observed taxa accumulation curves of primary and secondary forest at different substrate and season: (A) branch; (B) leaf; (C) soil; (D) trunk; (E) all substrates per forest and (F) all substrates per season. Agaricales based on the mean of 1000 randomized orderings of sample number.

TABLE 1. *Fisher's alpha computed for Agaricales basidiome communities.*

| | Taxa | Individuals | α |
|---|---|---|---|
| Trunk | | | |
| Primary | 28 | 40 | 41.45 |
| Secondary | 23 | 34 | 31.22 |
| Branch | | | |
| Primary | 54 | 91 | 55.87 |
| Secondary | 54 | 90 | 57.00 |
| Leaf | | | |
| Primary | 84 | 178 | 62.13 |
| Secondary | 89 | 146 | 96.75 |
| Soil | | | |
| Primary | 53 | 63 | 157.61 |
| Secondary | 22 | 28 | 47.37 |
| Total | | | |
| Primary | 186 | 369 | 149.64 |
| Secondary | 160 | 298 | 140.69 |
| Rainy season | | | |
| Primary | 177 | 329 | 156.11 |
| Secondary | 155 | 286 | 138.22 |
| Dry season | | | |
| Primary | 29 | 43 | 39.07 |
| Secondary | 9 | 12 | 16.36 |

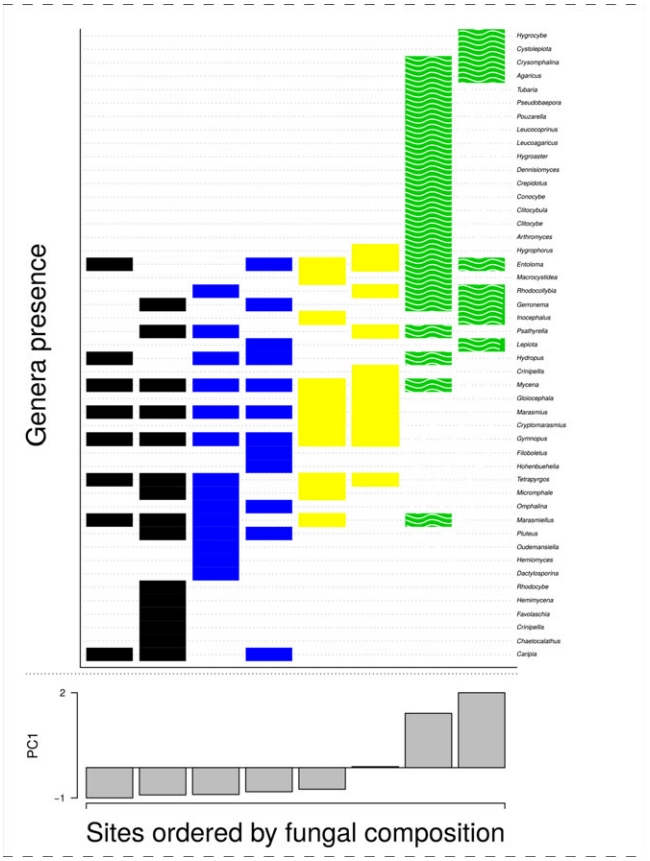


FIGURE 3. Histogram of generic composition. Forests (columns) were ordered by their scores in the first PCA axis representing changes in species composition. PCA was conducted using the similarity measures based on the Jaccard index modified by Chao *et al.* (2005). Species were ordered by their average position along the first PCA axis. Black = Branch, Yellow = Leaf, Green with wavy white line = Soil, Blue = Trunk.

Species accumulation curves.—A majority of the species (247; 85%) were singletons (*e.g.*, a single basidiome recorded one time during the course of the survey), of which 170 (58.6%) were observed during first-year censuses and 53 (18.3%) in the second year. Rarefaction curves illustrate that saturation was not attained in any forest type, substrate, or season (Fig. 2A–F). However, at the highest sampling intensity, the number of singletons decreased relative to doubletons, suggesting the species accumulation curves were becoming asymptotic.

Furthermore, less than one-fifth of the taxa were repeat observations among years and these include common taxa such as *Caripia montagnei*, *Gloiocephala epiphylla*, *Marasmius phaeus*, *Mycena chloroxantha*, *Mycena spinosissima*, and *Tetrapyrgos longicystidiata* which were shared among all forest plots. Most taxa belong to the genera *Marasmius* (78 spp.), *Mycena* (38 spp.), and *Gymnopus* (30 spp.) principally inhabitants of leaf litter and branches (Fig. 3). The most common taxa were *Mycena ixoxantha* Singer, *M. spinosissima*, and *Mycena* "yellow1".

Basidiome composition in relation to substrate, forest type and year.—Although 81 percent (234) of all taxa were recorded as unique to either primary or secondaryforest plots (Table S1), substrate type overshadowed forest plot history in driving compositional variation (Figs. 3 and 4). Overall, variation in basidiome community composition was more conserved among substrate types than by forest history or season (Fig. 4). Specifically, basidiome assemblies occurring on soil and leaf litter were more conserved among forest types than larger necromass (trunks and branches) as illustrated by the large overlap for these groups (Fig. 4A). PCoA ordination resulted in an explained variance of 79 percent for the first ordination axis.

## DISCUSSION

Fungi are vital contributors tonutrient cycling and decomposition of organic material in forests worldwide (Smith & Read 1997) and they are an important, albeit frequently cryptic, component of tropical biodiversity (Arnold & Lutzoni 2007, Aime & Brearley 2012). However, little is known about the sensitivity of tropical macrofungi to anthropogenic disturbances such as deforestation and climate change. By surveying experimentally managed and primary forests, we have made a first pass at understanding how fruiting phenology of four Amazonian understory fungal guilds vary in relation to rainfall and recent (<30 yr) anthropogenic disturbance.

During the course of a two-year intensive survey, species-accumulation curves did not saturate for any of the studied fungal guilds in either forest condition. Non-saturation of species

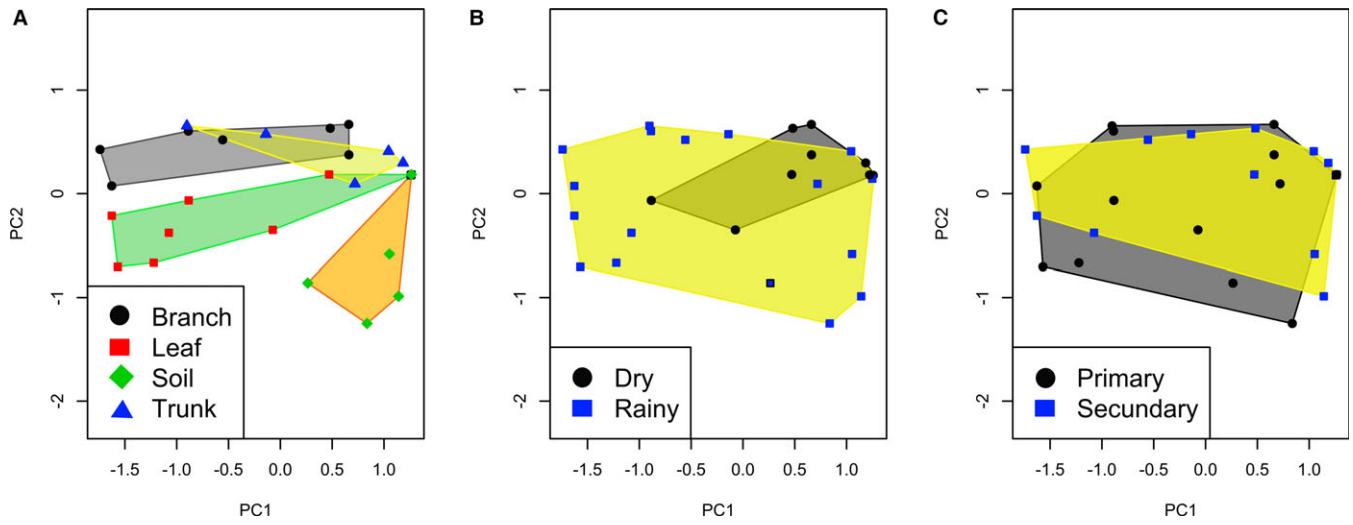


FIGURE 4. Principal Coordinates Analysis plots showing fungal communities according to: (A) substrate; (B) season; and (C) forest.

accumulation curves in fungal diversity assessments has been commonly reported from studies conducted in other regions (*e.g.*, Straatsma *et al.* 2001, Straatsma Straatsma & Krisai-Greilhuber 2003; Porter *et al.* 2008). Despite that, here we provide suggestive evidence of a synergistic effect of seasonality and forest history on basidiome community structure in Amazon forests as dry season fruiting communities of managed forest plots harbored significantly lower abundance and richness than those of the primary forests. Furthermore, we observed guild-dependent contrasting effects of forest management practices on basidiome richness. Although secondary forests harbored greater basidiome richness for leaf-inhabiting fungi they show a concomitant reduction in the soil community suggesting that changes in Amazonian basidiome community structure are possibly linked to different decay processes of necromass and leaf litter in relation to anthropogenic disturbance (Mesquita *et al.* 1997, Feldpausch *et al.* 2004, Vasconcelos & Laurence 2005).

Only one-fifth of the recorded taxa were shared between secondary and primary forest plots alike and these were tightly conserved within substrate guilds, especially those of leaf litter and soil communities. However, whether high species turnover among forest types and survey year reflects changes in substrate quality brought about by forest management practices, or due to incomplete sampling cannot be fully disentangled within the framework of this study. Nonetheless, composition was conserved within substrate types and among forest types suggesting that potential niche shifts due to altered environmental conditions are not responsible for compositional changes among secondary and primary forest plots.

SAMPLING INTENSITY AND TAXA SATURATION IN AMAZONIANBASIDIOME COMMUNITIES.—The fact that most species-accumulation curves do not saturate was not unexpected. Similar results from long-term surveys on equivalent sized plots in temperate regions such as Switzerland (21-yr) and Austria (7-yr) also failed to attain saturation (Straatsma *et al.* 2001, Straatsma & Krisai-Greilhuber 2003). In Panama and Colombia as well, short-term (2-yr) basidiome surveys conducted in both primary and secondary forests also reported accumulation curves that failed to reach asymptote (López-Quintero *et al.* 2012, Piepenbring *et al.* 2012).

Indeed, a majority of the recorded taxa in this study were singletons. This fact, in combination with the high inter-annual taxa turnover and the cryptic nature of fungi, may explain why species-accumulation curves did not saturate. In a nearby central Amazonian forest Braga-Neto *et al.* (2008) observed that only 37 percent of the marasmioid fungi were repeats over a 1-year period suggesting that turnover may be more related to seasonal differences in fungal fruiting phenologies. Certainly, repeat surveys and diversified sampling strategies may optimize species detection and offer insights in long-term temporal variation in the fruiting regimes of these cryptic and ephemeral taxa (Bills & Polishook 1994, Coddington *et al.* 1996, Sørensen *et al.* 2002, Yamashita *et al.* 2015). Despite that, little remains known about macrofungal distribution patterns in tropical regions, and even less so in Amazonia as even meso-scale patterns of spatial turnover in fruiting fungi composition are shown to be staggeringly high. For example, in the genus *Marasmius* (large groups of leaf litter fungi of lowland tropical forests) less than 40 percent of the morphospecies documented from Adolpho Ducke Ecological Reserve (reserve 5 in Fig. S1), *ca* 30 km distant from the BIONTE site, were shared taxa with this study (Braga-Neto *et al.* 2008; D. L. Komura, pers.obs.). Such high beta diversity of Agaricalean taxa in central Amazonia clearly illustrates the taxonomic challenges associated with researching macrofungi in this region.

GUILD DEPENDENT EFFECTS OFFOREST HISTORY ON FRUITING COMMUNITIES.—The importance of forest age on fungal composition has been suggested to be linked to habitat differences associated with ontogeny of tree species and its subsequent effects on

local microenvironments (Lodge & Cantrell 1995). For example, Cowley (1970) showed that microfungal communities in decomposing leaf litter at Puerto Rico were sensitive to stress induced by canopy openings and irradiation. Thus, disturbances that disrupt the canopy contribute to spatial as well as temporal impacts on decomposer fungi guilds particularly for basidiomycetes with superficial mycelia especially sensitive to drying (Hedger 1985). However, multivariate analyses from both presence-absence and abundance data suggest here that substrate specific differences in macrofungi fruiting community structure overshadow those of management practice.

Changes in physicochemical properties of soils due to the compaction process of timber extraction have also been shown to be positively associated with soil mycelial communities such as saprobes and parasites whereas negatively associated with ectomycorrhizal guilds (Hartmann *et al.* 2014). However, soil and leaf litter fungal guilds in this study varied less compositionally than that of trunks. In temperate regions, spatial aggregation of rotting log communities is partitioned within rather than among logs (Kubartová *et al.* 2012), suggesting that the composition of chance early colonizers in concert with the subsequent species interactions results in a metacommunity dynamic (Jenkins 2006), which promotes spatially patchy occupancy patterns (Gilbert & Sousa 2002, Gourbiere & Gourbiere 2002). Likewise, macrofungi of larger necromass such as downed trunks and logs undergo succession as decomposer composition shifts in concert with the quality of substrate changes caused by decay (Allen *et al.* 2000).

The comparatively higher taxonomic richness of leaf litter communities of secondary forests could be explained by the greater presence of desiccation resistant genera such as *Marasmius*, *Marasmiellus*, *Tetrapyrgos*, and *Micromphale* (Lodge & Cantrell 1995). In Amazonia, leaf litter fall and decomposition rates are shown to differ among primary and secondary forests (Barlow *et al.* 2007) and, for example, Mesquita *et al.* (1997) reported relatively slower leaf litter decomposition rates in secondary versus primary forests, suggesting that greater litter accumulation in secondary habitats may equate to greater substrate diversity for macrofungal leaf litter assemblages. Indeed, greater substrate quantity of fallen leaves in managed forests and their relatively faster turnover times (Reich *et al.* 2004) may also contribute to elevated local diversity of leaf inhabiting fungi in secondary forests.

Implications of forest management and seasonality on amazonian fruiting macrofungi.—Macrofungi play a crucial role in the biogeochemical cycles of forest's worldwide and potential impacts from anthropogenic disturbances on their communities, which may include forest management practices, can alter their structure in complex ways. The greatest challenge to accurately characterizing macrofungal communities is surmounting their high level of cryptic diversity as basidiome communities represent only a mere fraction of the mycelial community (Porter *et al.* 2008). A comprehensive assessment of macrofungal communities demands implementation of either long-term monitoring programs involving multiple sampling protocols (Yamashita *et al.* 2015), use of genetic screening techniques (Hartmann *et al.* 2014) or combinations therein.

A majority of the taxa observed in this study were restricted to either one of the two forest types as singletons suggesting that spatial patterns of basidiome distributions may be larger than the spatial scale of the experimental design of the study area. Nonetheless, macrofungal fruiting richness and frequency were disproportionately reduced in secondary forests during the dry season. Considering models predict that Amazonian dry seasons will intensify (Lewis *et al.* 2011) our results point to the sobering possibility that basidiome production of macrofungal communities in secondary forests throughout the Amazon Basin may reduce significantly. Such a prospect would inevitably compromise the potential for genetic recombination and dispersal: both of which are fundamental for long-term survivorship of a species.

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## DATA AVAILABILITY

Data available from the Dryad Repository: http://dx.doi.org/10.5061/dryad.td30f (Komura *et al.* 2017).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Chaodist.R: Functions to calculate dissimilarity between sets of communities using the metrics corrected for undersampling.

TABLE S1. *Taxa list and distribution of Agaricales in the BIONTE study plots in a central Amazonian forest.*

FIGURE S1. Location and experimental design of BIONTE's Project site in central Amazonia.

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