


Does soil pyrogenic carbon determine plant functional traits in Amazon Basin forests?

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Abstract Amazon forests are fire-sensitive ecosystems and consequently fires affect forest structure and composition. For instance, the legacy of past fire regimes may persist through some species and traits that are found due to past fires. In this study, we tested for relationships between functional traits that are classically presented as the main components of plant ecological strategies and environmental filters related

to climate and historical fires among permanent mature forest plots across the range of local and regional environmental gradients that occur in Amazonia. We used percentage surface soil pyrogenic carbon (PyC), a recalcitrant form of carbon that can persist for millennia in soils, as a novel indicator of historical fire in old-growth forests. Five out of the nine functional traits evaluated across all 378 species were correlated with some environmental variables. Although there is more PyC in Amazonian soils than previously reported, the percentage soil PyC indicated no detectable legacy effect of past fires on contemporary functional composition. More species with dry diaspores were found in drier and hotter environments.

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We also found higher wood density in trees from higher temperature sites. If Amazon forest past burnings were local and without distinguishable attributes of a widespread fire regime, then impacts on biodiversity would have been small and heterogeneous. Alternatively, sufficient time may have passed since the last fire to allow for species replacement. Regardless, as we failed to detect any impact of past fire on present forest functional composition, if our plots are representative then it suggests that mature Amazon forests lack a compositional legacy of past fire.

Keywords Fruit type · Wood density · Fire · Soil charcoal · Climatological water deficit · Temperature · Elevation

Introduction

Throughout global tropical forests, fire is now often used to facilitate broad-scale clearing of the rain forest frontier. Although there is little understanding about the scale and frequency of past fires, historical fires may have been more localized than today, with anthropogenic fires used for opening and maintaining gaps for agriculture, hunting and gathering, and

perhaps influencing plant succession through management of secondary vegetation (Barton et al. 2012; McMichael et al. 2012; Watling et al. 2017) and with natural fires coinciding with the driest periods of Amazonian history (Bush et al. 2008). Charcoal records suggest fire return intervals on the order of 200–1000 years during the Holocene and occurring as recently as 250–390 years before present in some old-growth moist Amazonian forest (Sanford et al. 1985; Turcq et al. 1998; Urrego et al. 2013). Climate reconstructions indicate that Amazon-wide drying occurred at frequent multi-year intervals over the last 10,000 years (Moy et al. 2002), likely modifying fire patterns. The presence and importance of fires in natural forests soils of the Amazon Basin may be indicated through soil pyrogenic carbon (PyC), produced by the incomplete combustion of organic matter, and which can persist in soils for millennia (Bird et al. 2015). Koele et al. (2017) estimated PyC for Amazonian forests to be 1.10 Pg (ha⁻¹) over 0–30 cm soil depth, about ten times larger than previously estimated by Bird et al. (2015). Fires occurring over the past few decades in the Amazon have resulted in substantial effects on forest dynamics and structure (Barlow and Peres 2008). However, there is little information about whether fire caused by climate variation and/or past human occupation

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in Amazon has had considerable legacy effects on present-day forest structure, composition, and functioning.

Hardesty et al. (2005) classified the Amazon region as a fire-sensitive ecosystem, which is damaged by fire that disrupts ecological processes, kills many individuals, or even eliminates species that have not evolved under this selective force. Undisturbed moist forest rarely burns (Uhl et al. 1998); however, forests that have burned once are more likely to burn again (Cochrane et al. 1999). The widespread historical impact of humans and fire on Amazonian forests is widely debated (McMichael et al. 2012) and remains entirely unaccounted in many influential studies (McMichael et al. 2017). Thus, even if fires were not a frequent environmental filter in these forests, they might have assembled species with a restricted range of functional traits related to fire in current forests, as has occurred in savannas (Dantas et al. 2013), making the forests more resilient to recent burning or to recent dry periods than previously thought. As a result of this environmental filter (fire), the structure, species composition, and functional traits (any attribute that has potentially significant influence on plant establishment, survival, and fitness: Reich et al. 2003) of forests of the Amazon Basin may have changed dramatically with time. Thus, studying these traits is fundamental, as they can provide a mechanistic basis for understanding how ecosystems function (Cadotte et al. 2015) and, specifically in this study, whether these traits can potentially reveal how the Amazon Basin forest community relates to fire and climate.

Determining the causative forces shaping contemporary forest composition faces methodological challenges. Determining the date of the last fire in old-growth forests through AMS Radiocarbon methods can be cost prohibitive. And fire can co-vary with climate, which can affect forest structure, composition, and dynamics (Esquivel-Muelbert et al. 2016; Feldpausch et al. 2011; Marimon et al. 2014). Previous studies evaluating whether fire is an evolutionary pressure shaping plant traits suggested that it may not always be possible to distinguish between traits that are adaptations originating in response to fire or exaptations originating in response to other factors (Bradshaw et al. 2011; Keeley et al. 2011). Thus, we must stress here that we do not intend to separate fire traits from aridity or soil infertility traits as it is

difficult to unambiguously isolate fire effects from these other influences.

Dry-vegetation and fire-prone species, which appear to invest more in fire resistance, have a preponderance of dry and small seed species and seasonal fruiting phenology, contrasting with rain forests species that have mainly larger, fleshy fruits and aseasonal seed dispersal (Vieira and Scariot 2006). Other authors contrasting savanna and forest vegetation have shown that leaf traits (larger leaves in forest species: Hoffmann et al. 2012) and tree height (higher in forest species: Hoffmann et al. 2003), as well as wood density, are, or could be, fire- or disturbance-related traits (Cianciaruso et al. 2012; Lucena et al. 2015). The few studies that have compared species traits across Amazonian sites commonly attribute differences in some traits to climatic and soil variations. For example, Malhado et al. (2015) showed Amazonian trees with smaller seeds occurring more frequently in transitional or seasonal forests, and genera with larger seeds more associated with climatically stable rain forests (low seasonality in temperature and precipitation). Quesada et al. (2012) found that basin-wide differences in stand-level turnover rates are mostly influenced by soil physical properties with variations in wood production mostly related to soil phosphorus status.

Understanding the disturbance history in tropical forests is vitally important for interpreting their present-day structure, composition, and dynamics. One of the main drivers of past change in the Amazon biome may have been fire (Pinter et al. 2011). Our study introduces a new important potential predictor to determine plant trait distributions across the Amazon Basin, soil PyC abundance. An understanding of soil PyC distribution may provide a large-scale perspective of fire history (Whitlock and Larsen 2001). Thus, our objective in this study was to assess the relationships between vegetation traits and environmental filters, accounting for climate and historical fires (PyC) across representative samples of the Amazon rain forest. We hypothesized that, despite the Amazon biome being a fire-sensitive ecosystem, some functional traits persist in modern old-growth rain forest vegetation as a legacy of past fire regimes. Specifically, we hypothesized that functional traits representative of species growing in fire-prone environments, such as higher wood density and shorter trees (Brando et al. 2012), are positively associated

with soil PyC abundance and that functional traits that respond to dry climate such as high numbers of dry fruit-type species and seasonal fruiting (Sfair et al. 2016) are related to drier and hotter climate conditions.

Materials and methods

Forest sites

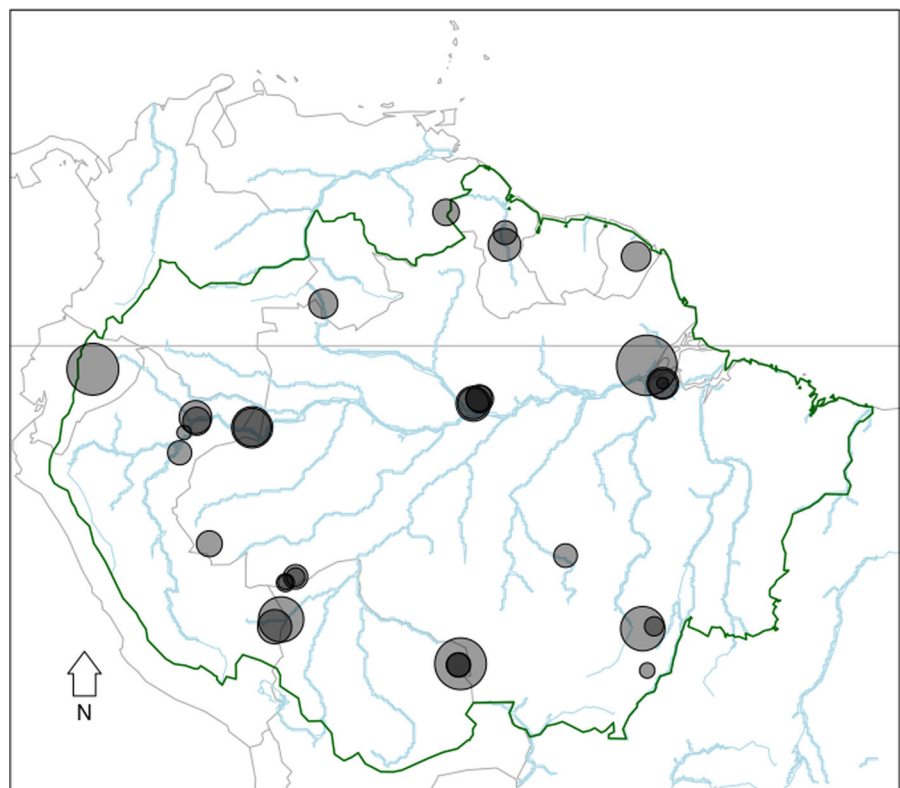
Species richness and individual abundance data from 34 1-ha permanent forest plots across the range of local and regional environmental gradients that occur in Amazonia were used in our analysis (Online Resource 1 and Fig. 1). The forest data, including *Terra Firme* forests on both clay-rich and white-sand substrates, and seasonally flooded forest are summarized in Online Resource 1. Of these 34 plots, 33 are in the ForestPlots.net database, a web repository for long-term tropical forest inventory plots, where trees ≥ 10 cm in diameter within an area are individually identified, measured, and tracked through time

(Lopez-Gonzalez et al. 2009, 2011), and one is in the Tropical Ecology Assessment and Monitoring (TEAM) database (MPEG 2014, VEGCAX1). All sites examined were old-growth humid forests, excluding Anthropogenic Dark Earth sites (*Terra Preta de Índio*). Based on the vegetation and local information, there was no evidence of recent, major, direct human impact or fire. The most abundant species in each plot (more than five individuals per plot) were chosen for analysis.

Plant traits

We selected six plant functional traits that are classically presented as the main components of plant ecological strategies (Pausas and Lavorel 2003). Some traits are strategies for disturbance and regeneration like fruit size and leaf length (Kraft et al. 2008), some are useful to understand plant response to fire such as tree height and wood density (Brando et al. 2012), and some are linked to climate as seed type (dry- versus fleshy-type fruits) and fruiting phenology (duration and timing of each phenophase) (Correa et al. 2015).

Fig. 1 Location of the Amazonian study sites (circles) showing the variation in percentage pyrogenic carbon in total soil. The green outline shows Amazonian boundary, blue lines are the rivers and streams. Circles are proportional to the percentage pyrogenic carbon in soil samples (0–30 cm interval) and are semi-transparent to visualize when overlapping



Seed type was extracted from several studies (mainly Amaral et al. 2009; Muniz 2008; Stefanello et al. 2009; Yamamoto et al. 2007). If a species could not be found in published studies, fruit type was drawn from genus-level information; it is well known that reproductive traits show clustering in phylogenetic trees (Chazdon et al. 2003). All fruit morphologies of the genera were checked in books, manuscripts, and published floras. We estimated fruit size and leaf length and we assessed maximum plant height based on botanical registers at Lista de Espécies da Flora do Brasil (<http://www.floradobrasil.jbrj.gov.br/>) and speciesLink Network (<http://splink.cria.org.br/>). For these previous parameters, we used at least ten different plants, including rarer individuals (smaller and bigger ones). If the differences between individuals were high, we expanded the sample collection. Wood density was obtained from Forestplots.net database or, when the species was absent, from the Wood Density database (Ketterings et al. 2001; <http://www.worldagroforestry.org/output/wood-density-database>).

Fruiting phenology was assigned based on the months that the species were collected with fruits on botanical registers at Lista de Espécies da Flora do Brasil (for species that were over-collected we selected the months with highest numbers of exsiccatae). We could not relate collections to specific plot locations, and thus we treated plant registers of different sites as originating from the same location. Although the timing of seasonal events, such as fruiting, is highly sensitive to climate (Chuine 2010) since collections cover a wide range of dates, the data should represent general phenology patterns for most species. Two phenology traits were derived from the survey: duration given by (i) number of days—number of months that the species was recorded as having fruit multiplied by 30 and (ii) fruiting timing occurring in the dry and/or wet periods—dry period, if a reproductive phenophase was registered between July and November, it was said to be in the dry period (seasonality defined according to Huete et al. 2006 in a multiple-scale study including an extensive 2000-km climate transect through eastern and central Amazonia), wet period, if registered between December and June, or both periods, if the phenophase was registered in mixed periods. The 34 studied plots include a wide geographic range with different seasonality calendars (Girardin et al. 2016), from

Guyana to Ecuador to the south border of Amazonia in Mato Grosso state. These different calendars have different dry and wet periods, and it is methodologically challenging to determine phenology including such site-specific variations. For this reason, we chose only one dry and wet period for the whole Amazon region, defined according to the previously mentioned study. Flowering phenology was not evaluated since it was found for less than half of all species.

Environmental variables

We considered three types of variables: climatic, topographic, and fire history-related. We used three climate predictors from WorldClim 1.4 dataset (Hijmans et al. 2005; <http://www.worldclim.org/bioclim.htm>): bio01 (annual mean temperature), bio05 (maximum temperature of the warmest month), and bio12 (annual precipitation) and a complementary measure of drought severity, the maximum climatological water deficit (MCWD; Aragão et al. 2007). These are some of the parameters considered to be critical to the physiological functioning and survival of plants (Woodward 1987). For altitude, we used Ambdata dataset (Amaral et al. 2013; <http://www.dpi.inpe.br/Ambdata/>). We used Pyrogenic Carbon (PyC) abundance as a proxy of past fire events, because it is estimated that up to 15% of fire-affected biomass is converted into pyrogenic organic carbon (Santín et al. 2015). We used PyC analysis rather than more time-intensive physical assessments of charcoal abundance based on counting or mass estimates of charcoal. AMS radiocarbon dating is expensive and usually only possible for a limited number of sites (we have charcoal dates for three study sites). PyC abundance, as percentage PyC of the soil sample, was quantified as stable polycyclic aromatic carbon (SPAC) analyzed via hydrogen pyrolysis (HyPy). The HyPy technique has been described elsewhere (Meredith et al. 2012) and the same experimental procedure was used in this study. PyC was quantified in the 0–30 cm soil interval (Koele et al. 2017).

Data analyses

The relationships between species traits and environmental variables were tested by RLQ combined with fourth-corner analysis (Kleyer et al. 2012; Dray et al. 2014). This analysis aims to investigate the relationships between two tables, R (environmental

characteristics) and Q (species attributes, in our case), using a third table, L (species abundance matrix), to establish the linkage and their combined ordination. R represents a matrix whose rows are the sites and columns the environmental characteristics for each plot; Q represents a matrix whose rows are tree species abundance and columns are the attributes for each species; L represents a matrix whose rows are plots and whose columns are tree species. Each matrix was primarily analyzed in isolation by means of a principal component analysis (PCA) for environmental data and traits, and according to a correspondence analysis (CA) for species abundance matrices. The relation among these matrices was established by means of a co-inertia analysis to maximize their covariance.

We followed the new approach recommended by Dray et al. (2014) in applying the fourth-corner tests to the output of the RLQ analysis, which allows for quantification and statistical testing of the relationships between environmental variables and species traits by means of two null models. We used a combination of model 2—which tests for the links between the matrices L and Q, with the null hypothesis assuming that the distribution of species with fixed (i.e., species-independent) traits is not influenced by environmental conditions—with model 4—which tests for the links between L and R, with the null hypothesis considering that the species composition with fixed environmental conditions is not influenced by species traits. According to the aforementioned authors, this new approach combining these two permutation models has correct type I error rates, but at the same time, as ter Braak et al. (2016) stated, it does not consider spatial, temporal, and phylogenetic autocorrelation. Significance of the relationship between species traits and environmental variables was assessed based on 999 permutations. All analyses were performed using the *ade4* package for R v.3.2.1 (R Core Team 2013).

Results

Our dataset represented 9789 individuals distributed across 378 species and the 34 old-growth forest plots. Of this total, 173 species had few individuals (less than ten individuals in only one or two plots). The ten most common species (according to frequency in plots and abundance) were *Tetragastris altissima*

(Burseraceae), *Iriartea deltoidea* (Arecaceae), *Euterpe precatória* (Arecaceae), *Pseudolmedia laevis* (Moraceae), *Eschweilera coriacea* (Lecythidaceae), *Amaioua guianensis* (Rubiaceae), *Cheilochlinium cognatum* (Celastraceae), *Socratea exorrhiza* (Arecaceae), *Rinorea guianensis* (Violaceae), and *Miconia pyrifolia* (Melastomataceae).

Plant traits varied according to the sites (Table 1): fleshy fruit species were dominant in most sites with two exceptions, ELD-01 and FMH-01, which were the more easterly sites (Venezuela and Guyana) (Fig. 1). Fruit length ranged from 2.1 to 8.8 (mean 3.9) cm across the sites, tree height from 18 to 28 (23) m, leaf length from 10 to 22 (13) cm, and wood density from 0.50 to 0.81 (0.65) g cm⁻³. Fruiting phenology by site was staggered through the year.

The first axis of the RLQ analysis accounted for 80.3% of the total co-inertia (i.e., the link between the traits and climatic variables) and the second axis for 14.7% (PyC). This represented 5.3% of the correlation expressed for the first axis in the CA of species composition (Table 2: L table), and 48.0 and 27.7% of the total variance expressed for the first axis in the PCA of the environmental variables (Table 2: R table) and functional traits (Table 2: Q table), respectively, indicating variability in species trait values across the environmental gradient.

Among those traits, only the variability in diaspore type and wood density was explained by the variability in the environmental gradient ($r = 0.89$, $p = 0.001$ and $r = -0.60$, $p = 0.001$, respectively; Fig. 2). And among these environmental parameters, average temperature ($r = -0.85$, $p = 0.001$), water deficit (MCWD) ($r = -0.89$, $p = 0.001$), annual precipitation ($r = -0.76$, $p = 0.001$), and altitude ($r = 0.87$, $p = 0.001$) explained the variability in the studied functional traits. There was also a significant association between PyC ($r = -0.71$, $p = 0.001$) and maximum temperature of the warmest month ($r = 0.88$, $p = 0.001$) with the second RLQ axis, but with traits unrelated to this axis, which may indicate a lack of detectable effect of past fires on contemporary composition and functioning of Amazon Basin forests (Fig. 2).

We also found a significant relationship between species composition and environmental variables (model 2, $p = 0.007$) and between species composition and functional traits (model 4, $p = 0.009$). These results indicate that species composition is dependent

Table 1 Vegetation trait descriptions of 34 forest plots in Amazonia

Plot	Species/ individuals	Leaf length (cm)	Maximum tree height (m)	Wood density (g cm ⁻³)	Fruit type	Fruit size (cm)	Fruiting timing
AGP-01	15/128	15	24	0.60	4 dry 10 fleshy 1 unk	3.2	Oct, Feb d, w
AGP-02	11/100	17	24	0.56	4 dry 6 fleshy 1 unk	3.4	Feb, w
ALF-02	22/430	13	24	0.61	1 dry 21 fleshy	3.6	Oct, d
ALP-30	20/356	12	20	0.62	7 dry 13 fleshy	4.2	Dec, w
BDF-03	22/198	12	27	0.68	9 dry 13 fleshy	3.2	Nov, d
BDF-09	24/196	11	26	0.70	9 dry 15 fleshy	2.7	Nov, d
BNT-02	23/253	12	25	0.72	8 dry 15 fleshy	4.6	Jan–Feb, w
BNT-04	22/274	13	28	0.72	8 dry 14 fleshy	3.5	Nov, d
CAX-01	20/268	10	23	0.74	7 dry 13 fleshy	3.3	Oct–Dec d, w
CAX-06	13/129	11	27	0.78	6 dry 7 fleshy	3.9	Nov, d
CUZ-01	25/319	13	18	0.53	2 dry 23 fleshy	4.9	Feb, w
DOI-01	18/207	16	25	0.66	6 dry 12 fleshy	3.2	Sep–Oct, d, w
DOI-02	8/73	17	24	0.61	3 dry 5 fleshy	8.8	Oct, d
ELD-01	6/82	11	22	0.75	5 dry 1 fleshy	5.1	Jan, Mar, w
FLO-01	27/500	14	20	0.63	4 dry 23 fleshy	3.1	Oct, d
FMH-01	13/394	10	28	0.81	6 dry 6 fleshy	4.2	Oct, d
HCC-21	20/489	14	20	0.57	5 dry 15 fleshy	3.6	Mar, w
IWO-22	12/328	10	22	0.81	5 dry 7 fleshy	5.5	Dec, w
JAS-02	22/258	19	24	0.53	5 dry 17 fleshy	3.5	Oct, d
JEN-11	24/229	12	26	0.65	10 dry 16 fleshy	4.1	Jan, w
JRI-01	32/327	14	25	0.69	7 dry 25 fleshy	3.2	Jan, w

Table 1 continued

Plot	Species/ individuals	Leaf length (cm)	Maximum tree height (m)	Wood density (g cm ⁻³)	Fruit type	Fruit size (cm)	Fruiting timing
LFB-01	20/460	14	21	0.58	5 dry 15 fleshy	2.7	Oct, d
LFB-02	18/435	15	21	0.55	5 dry 13 fleshy	3.2	Oct, d
NOU-06	7/89	17	27	0.64	1 dry 6 fleshy	2.9	Oct, Jan d, w
POR-01	25/293	14	22	0.62	5 dry 20 fleshy	2.9	Oct, d
POR-02	23/270	12	22	0.64	4 dry 19 fleshy	3.1	Aug–Oct, d
RST-01	12/195	13	19	0.50	1 dry 11 fleshy	7.0	Jul–Aug, d
SCR-05	30/460	12	25	0.71	7 dry 23 fleshy	5.2	Jan, w
SUC-02	19/164	15	21	0.62	5 dry 14 fleshy	4.2	Oct, d
TAM-05	28/317	13	23	0.60	5 dry 23 fleshy	2.8	Oct, d
TAN-04	21/509	12	19	0.63	3 dry 18 fleshy	2.1	Apr–May, w
TEC-01	19/214	11	25	0.78	6 dry 13 fleshy	2.9	Nov, d
VCR-02	19/560	11	19	0.66	2 dry 17 fleshy	2.9	Sep, d
YAN-01	19/225	22	26	0.56	7 dry 12 fleshy	4.8	Oct, d

unk unknown, *Jan* January... *Dec* December, *d* dry period, *w* wet period

on the environmental conditions (altitude, climate, and fire history) of the sites and influenced by species' functional attributes.

Species with denser wood were associated with hotter ($r = 0.28$, $p = 0.002$) and lower elevation environments ($r = -0.20$, $p = 0.037$); species with dry diaspores were associated with drier ($r = 0.23$, $p = 0.007$), hotter ($r = 0.18$, $p = 0.014$), and lower elevation environments ($r = -0.19$, $p = 0.01$); the opposite was found for the relationships between fleshy fruit species and MCWD ($r = -0.23$, $p = 0.008$), temperature ($r = -0.18$, $p = 0.017$), and altitude ($r = 0.19$, $p = 0.01$). There were less species fruiting in the dry period ($r = -0.16$,

$p = 0.042$) and the fruiting duration was shorter ($r = -0.17$, $p = 0.027$) in sites where annual precipitation was higher (Fig. 3). None of the studied traits were significantly associated with PyC (Fig. 3); however, the analyses showed a tendency for less species fruiting in the dry period in plots with higher percentage soil PyC ($r = -0.12$, $p = 0.091$; Fig. 4).

Discussion

Our results show that functional traits and environmental variables jointly predict variation in tree species composition in the Amazon Basin. The

Table 2 Results of RLQ analysis using environmental variables and species traits

	Axis 1 (%)	Axis 2 (%)
R table PCA	2.88 (48.02)	1.97 (32.89)
L table CA	0.95 (5.29)	0.93 (5.18)
Q table PCA	2.49 (27.67)	1.84 (20.48)
RLQ axes eigenvalues	0.54 (80.31)	0.098 (14.71)
Covariance	0.73	0.31
Correlation: L	0.30 (30.79)	0.21 (21.33)
Projected Variance: R	2.78 (96.66)	4.74 (97.71)
Projected Variance: Q	2.14 (85.87)	3.32 (76.70)

Eigenvalues (and % of total co-inertia) for the first two axes. Ordinations of tables R (principal components analysis—PCA), L (correspondence analysis—CA), and Q (PCA)

Summary of RLQ analysis: eigenvalues and percentage of total co-inertia accounted for by the first two RLQ axes, covariance and correlation (and % variance) with the correspondence analysis of the L matrix and projected variance (and % variance) with the R and Q matrices

findings of this study represent some of the main hyperdominant species that occur throughout the Amazon Basin (ter Steege et al. 2013) and dominant species in Cerrado–Amazon forest transition sites (Ackerly et al. 1989; Marimon et al. 2006; Mews et al. 2011; Morandi et al. 2016). The fourth-corner permutation models assessing the trait–environment–species link suggests that the distribution of species with fixed traits is influenced by environmental characteristics and that the species composition of sites with given environmental characteristics is influenced by species traits. Kraft et al. (2008), using a functional ecology approach, also found evidence for niche-based processes in an Amazonian forest. Other recent studies have shown that Amazonian tree species distribution responds strongly to environmental variation (Esquivel-Muelbert et al. 2016) and the strength of response is significantly correlated to functional traits (Rowland et al. 2014; Silva et al. 2014).

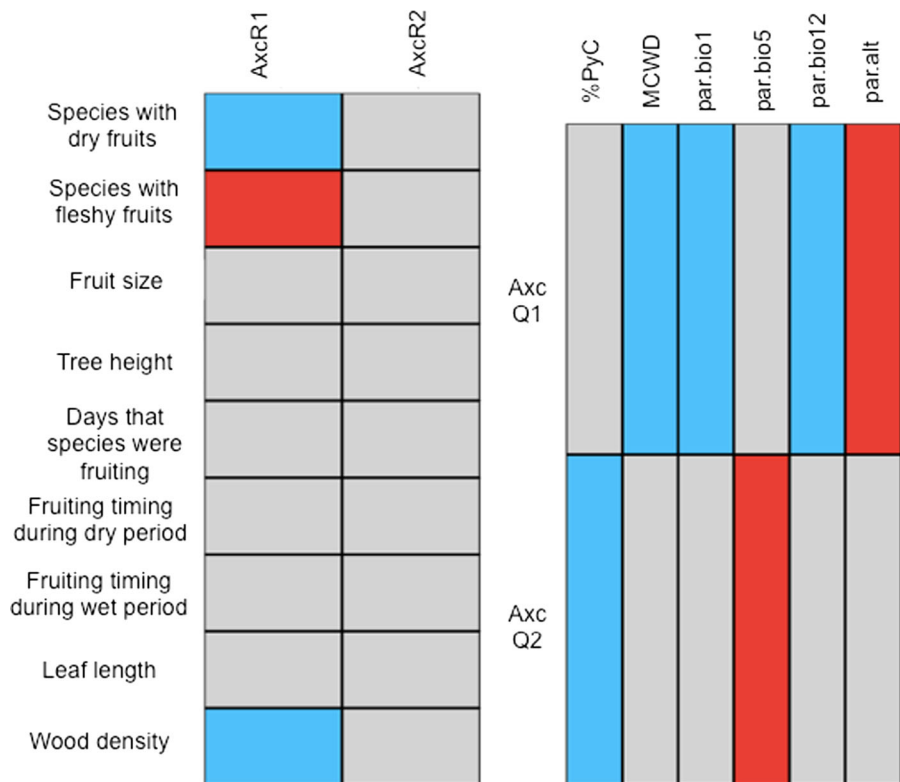
Differences in community structure and function were primarily driven by temperature and water availability (and altitude, variable usually correlated to the other two climate parameters: Benavides et al. 2016). Therefore, functional traits representative of fire-prone environment species such as higher wood density and shorter trees were not associated with soil PyC abundance. These results of no detectable legacy of fire effect on plant traits may be a consequence of

several factors: (i) historical fires may have been locally and/or temporally restricted and not associated with a widespread and/or frequent fire regime; therefore, impacts on biodiversity would have been small and/or heterogeneous; (ii) alternatively, sufficient time may have passed since the last fire (hundreds of years) to allow the forest to recover; and (iii) soil pyrogenic carbon storage may not be a suitable predictor of past fires. Despite this lack of detectable effect of past fires on contemporary composition and functioning of Amazon Basin forests, the significant relation between PyC and the second RLQ axis and marginal significance with one of the studied traits, suggests that more aspects of past fire events need to be investigated. Large-scale carbon radiocarbon dating, although cost prohibitive, would provide key information about time since last fire.

It has been shown that fire strongly mediated the effect of other environmental variables on some traits in a longleaf pine savanna in California, indicating that strong environmental gradients cannot be considered independently when assessing their effects on functional traits (Ames et al. 2015). However, savannas are fire-prone ecosystems, which evolved as a response of fire regimes, i.e., intensity, duration, and frequency of burnings (Bowman et al. 2009). In tropical rain forests, though, the data from charcoal radiocarbon dating imply a fire return of hundreds or thousands of years (Sanford et al. 1985; Turcq et al. 1998), with distinct spatial and temporal patterns (Bush et al. 2007, 2008). Some preliminary charcoal dating results of three studied plots may confirm this variability in return times and spatial patterns: an eastern Amazonia plot had fire estimates of 1134 years before present (BP) (charcoal in 10–20 cm) and 1620 years BP (30–50 cm); a northern Amazonia plot, 989 years BP (32 cm); and a south edge plot, a range of 96 years BP (10–20 cm), 806 years BP (20–30 cm), and 1372 years BP (150–200 cm). Other recent AMS results from the same region show a larger return interval in fire records for some sites, ~6000 years (from 6876 to 365 years BP: Goulart et al. 2017). Previous studies of soil charcoal have also shown a spatially localized and heterogeneous signature of fire on Amazon forests (McMichael et al. 2012, 2017).

Thus, rather than a pristine tropical forest, some areas in the Amazon Basin have been interpreted as constructed landscapes, dramatically altered by past indigenous groups (Erickson 2008; Heckenberger

Fig. 2 RLQ results between the first two RLQ axes for environmental variables (AxR1/AxR2) and traits (AxQ1/AxQ2). Significant ($p < 0.05$) positive associations are represented by red cells; significant negative associations by blue cells. Variables with no significant associations are shown in gray. *parbio1* annual mean temperature, *parbio5* maximum temperature of the warmest month, *parbio12* annual precipitation, *paralt* elevation, *MCWD* maximum climatological water deficit, *%PyC* percentage of pyrogenic carbon in total soil (0–30 cm depth)



et al. 2007; Roosevelt 2013) indicating propensity for regional forests to burn, especially during periods of drought (Bush et al. 2008). Anthropogenic fire has been a factor in shaping plant communities through human prehistory, e.g., generally a woody non-fire-prone vegetation type tends to transition to a more herbaceous, flammable, and shade-intolerant vegetation type with frequent fire (Pinter et al. 2011), changing forest composition (Barlow and Peres 2008) and structure (Bennett et al. 2013) and species abundance (Piperno and Becker 1996, depending on the regional pool of species: Mittelbach and Schemske 2015). Brando et al. (2014) presented the first evidence of substantial fire-induced tree mortality due to altered fire regimes and a widespread invasion by flammable grasses in a southern Amazonian forest subjected to experimental repeat burns. Besides fire-induced mortality, other demographic patterns also play important roles after a disturbance such as recruitment and growth of individuals. For these reasons, forest recovery is very slow (Almeida et al. 2016; Barlow and Peres 2008; Flores et al. 2012; Uhl et al. 1998). However, recovery may be fast enough to erase the signal of fire history on the functional composition of

this vegetation, considering the limited reported charcoal AMS dated fire spatiotemporal patterns with long times since last fire in old-growth forests. In fact, it may take only a decade for trait changes to be apparent at the individual level as a response to some stress, as van der Sande et al. (2016) found for wood density and specific leaf area in Neotropical forests subject to increased drought stress.

There is uncertainty about how PyC forms and persists in soils (Bird et al. 2015). PyC generation is governed by complex factors as investigated by Brewer et al. (2013): fuel properties (density, composition, arrangement, and moisture) and burning conditions (weather, flame height, and flame time). As a result, many low-intensity fires may not produce a similar amount of PyC in the soil, as few intense fires. Improved understanding of how different fire types affect PyC storage and the longevity of PyC in moist tropical forests will assist in the development of soil PyC as a proxy providing information about past fires.

Lowland Amazon tropical rain forests possess an annual climate that is warm with little temperature variation; rainfall, however, varies spatially and is

Fig. 3 Fourth-corner results between environmental variables and traits. Significant ($p < 0.05$) positive associations are represented by red cells; significant negative associations by blue cells. Variables with no significant associations are shown in gray. *parbio1* annual mean temperature, *parbio5* maximum temperature of the warmest month, *parbio12* annual precipitation, *paralt* elevation, *MCWD* maximum climatological water deficit, *%PyC* percentage of pyrogenic carbon in total soil (0–30 cm depth)

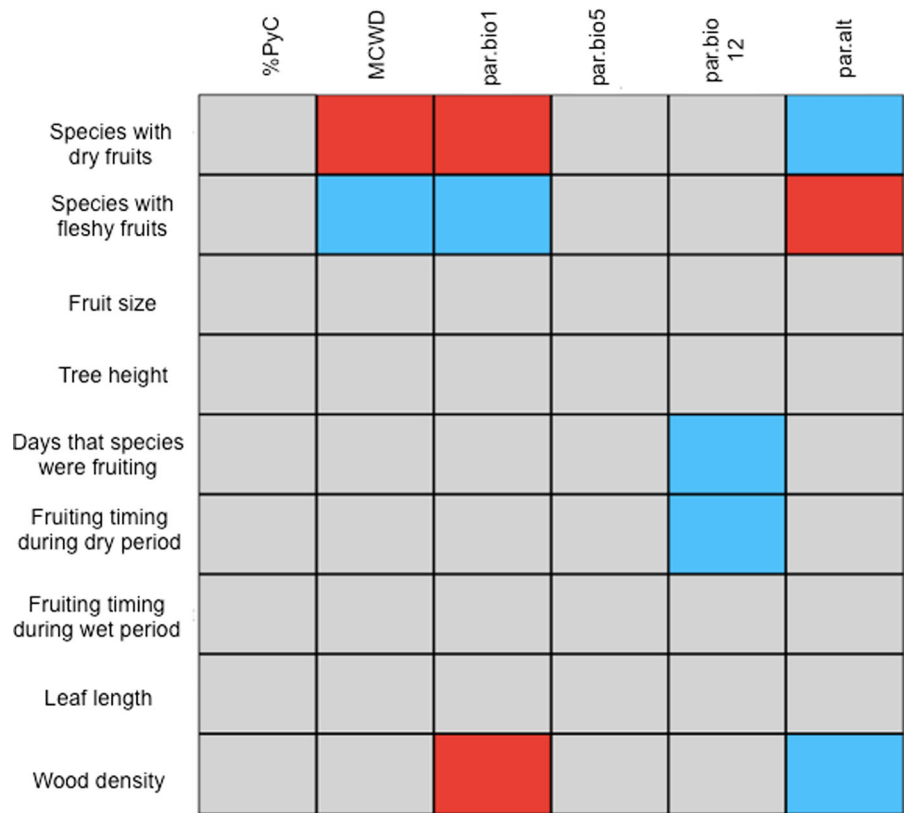
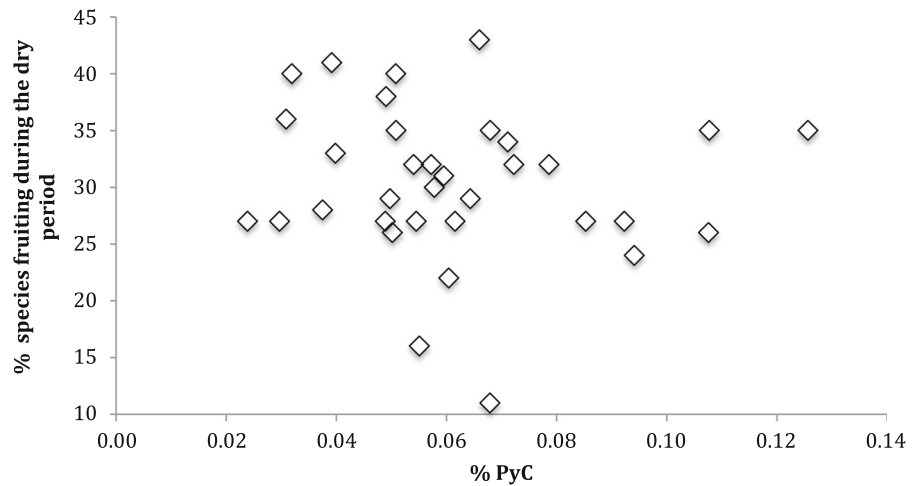


Fig. 4 Percentage of species fruiting during dry period plotted against percentage pyrogenic carbon in total soil



highly seasonal in some regions: the south and southeast are drier and more seasonal, while the west and northwest are wetter and aseasonal (Sombroek 2001). During the last century the Amazon warmed by 1 °C, but rainfall pattern changes are more difficult to identify (IPCC 2013). Climate change is viewed as a threat to biodiversity (Bellard et al. 2012). Despite

some resilience to moderate annual and repeated droughts (Davidson et al. 2012; Feldpausch et al. 2016), plant traits related to drought-induced mortality, such as lower wood density, larger tree size, fast-growing pioneers, and evergreens (Feldpausch et al. 2016; O’Brien et al. 2017; Phillips et al. 2009), may be not be advantageous in drier sites, thus highlighting

the need to identify traits that account for differential tree vulnerability to environmental stress.

We found more species with dry diaspores in drier and hotter environments, which may be an advantageous trait in disturbed forests. Moreover, the high number of wind-dispersed species in areas closer to Venezuela could be an imprint of ancient forest–savanna transitions (or dry forests). Other reviews have shown the importance of wind-adapted (Howe and Smallwood 1982) and dry fruit species in dry environments (van der Pijl 1972). Thus, in a future scenario of drier and hotter Amazonia, with fires possibly becoming more frequent (Alencar et al. 2015), these forests are likely to be replaced by wind-dispersed plants easily spread independent of animal vectors. Also, the light and flat primarily wind-dispersed seeds may also be transported long distances by water-mediated dispersal in lower altitude and flood-prone sites (Säumel and Kowarik 2013), which our results confirmed by the high number of dry seed species in lower elevations. We found that with higher precipitation, fewer tree species produced fruits in the dry period and the duration of fruiting in any period was shorter. In areas with higher precipitation, more fleshy fruit species are expected, which will develop and disperse their fruits during the wet period (Correa et al. 2015; Howe and Smallwood 1982). Even in a moist environment like the studied region, the amount of precipitation caused fruiting to be less spread throughout the year and more synchronous with the wet period.

Wood density was positively associated with average temperature and negatively with altitude, corroborating the findings of Quesada et al. (2012). Thus, our results support the theory that higher temperatures and lower altitudes induce a stress avoidance strategy by reducing hydraulic efficiency and vulnerability to xylem cavitation by increasing wood density (Swenson and Enquist 2007). Also, higher wood density species would be less susceptible to fire-induced mortality (Brando et al. 2012) in hotter and drier Amazon forests (Feldpausch et al. 2016; O'Brien et al. 2017; Phillips et al. 2009).

Five out of the seven functional traits evaluated across all 378 species were correlated with some environmental variables, indicating that the selected traits and the independent parameters were adequate in that they cover the range of traits commonly deemed essential to woody plant strategy (Pausas and Lavorel

2003). Despite this, fruit size, maximum height, average leaf size, and fruiting during the wet period did not relate to any parameter. Soil fertility (Clarke et al. 2016; Dantas et al. 2013) could have been an important environmental factor predicting variation of the studied traits. In fact, Koele et al. (2017) found positive associations between PyC and soil nitrogen and phosphorous for the studied plots and we also might expect functional traits to be influenced by edaphic factors as shown by Quesada et al. (2012) and Toledo et al. (2016) in the Amazon Basin. Additionally, including other fire-related traits such as bark thickness, leaf toughness, and height-to-diameter ratio of plant species might have relevance to future studies of Amazon Basin forest dynamics (Cianciaruso et al. 2012; Lucena et al. 2015).

In general, the Amazon forests examined in this study had higher proportions of zoochory (dispersal of seeds by animals) than other dispersal types and large-sized fruits, confirming the importance of animal-mediated seed dispersal in the tropics (Correa et al. 2015; Howe and Smallwood 1982). It has been shown that tree height and wood density vary significantly across Amazonia (Feldpausch et al. 2011; Nogueira et al. 2008), differences also reflected in the most abundant species of our study. The results also indicated that Amazon forests are predominantly populated by tree species with leaf sizes in the mesophyll class (Malhado et al. 2009). Lastly, fruiting was in different periods throughout the year, reflecting the high variation in the time of fruit production and maturation.

The long-term ecological consequences of fire in Amazon forests are not clear. Fires are rapidly becoming a common occurrence in vast areas of both disturbed and undisturbed Amazonian forests, and pyrogenic carbon analysis indicates that fire historically occurred in all our plots, including even the wettest plots of northwestern Amazonia, but the time-scale of these burnings seems to be longer than that needed for forest functional composition recovery. In this study, we observed that functional traits and environmental variables jointly predicted variations in tree species composition in Amazon Basin forests. We also showed the lack of a detectable effect of PyC on specific traits, but the existence of a secondary association with the general trait distribution (axis 2) indicates that the consideration of climatic variables alone may not be sufficient to explain species

distributions and the maintenance of diversity and functioning in Amazonian forests. The future trajectory of Amazonian forests that experience drought and fire will depend, in part, upon tree species composition and drought- and fire-tolerance traits, both of which still need to be better disentangled and understood.

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