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

2

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37 AP, DN, EV, EO, OLP, HS, HR-A, JC, LVF, NH, RVM, RB, SLL, WL and YM coordinated data collection

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59

60 ABSTRACT

61 Amazon forests are fire-sensitive ecosystems and consequently, fires affect forest structure and composition. For
62 instance, the legacy of past fire regimes may persist through some species and traits that are found due to past
63 fires. In this study, we tested for relationships between functional traits that are classically presented as the main
64 components of plant ecological strategies and environmental filters related to climate and historical fires among
65 permanent mature forest plots across the range of local and regional environmental gradients that occur in
66 Amazonia. We used percentage surface soil pyrogenic carbon (PyC), a recalcitrant form of carbon that can
67 persist for millennia in soils, as a novel indicator of historical fire in old-growth forests. Five out of the nine
68 functional traits evaluated across all 378 species were correlated with some environmental variable. Although
69 there is more PyC in Amazonian soils than previously reported, the percentage soil PyC indicated no detectable
70 legacy effect of past fires on contemporary functional composition. More species with dry diaspores were found
71 in drier and hotter environments. We also found higher wood density in trees from higher temperature sites. If
72 Amazon forest past burnings were local and without distinguishable attributes of a widespread fire regime, then
73 impacts on biodiversity would have been small and heterogeneous. Alternatively, sufficient time may have
74 passed since the last fire to allow for species replacement. Regardless, as we failed to detect any impact of past

75 fire on present forest functional composition, if our plots are representative then it suggests that mature Amazon
76 forests lack a compositional legacy of past fire.

77 Key-words: fruit type; wood density; fire; soil charcoal; climatological water deficit; temperature, elevation.

78

79

80 INTRODUCTION

81 Throughout global tropical forests, fire is now often used to facilitate broad-scale clearing of the rain
82 forest frontier. Although there is little understanding about the scale and frequency of past fires, historical fires
83 may have been more localized than today, with anthropogenic fires used for opening and maintaining gaps for
84 agriculture, hunting and gathering, and perhaps influencing plant succession through management of secondary
85 vegetation (Barton et al. 2012, McMichael et al. 2012, Watling et al. 2017) and with natural fires coinciding with
86 the driest periods of Amazonian history (Bush et al. 2008). Charcoal records suggest fire return intervals on the
87 order of 200-1,000 yrs during the Holocene and occurring as recently as 250-390 yrs before present in some old-
88 growth moist Amazonian forest (Sanford et al. 1985, Turcq et al. 1998, Urrego et al. 2013). Climate
89 reconstructions indicate Amazon-wide drying occurred at frequent multi-year intervals over the last 10,000 years
90 (Moy et al. 2002), likely modifying fire-patterns. The presence and importance of fires in natural forests soils of
91 the Amazon Basin may be indicated through soil pyrogenic carbon (PyC), produced by the incomplete
92 combustion of organic matter, and which can persist in soils for millennia (Bird et al. 2015). Koele et al. (in
93 review) estimated PyC for Amazonian forests to be 1.10 Pg (ha⁻¹) over 0-30 cm soil depth, about ten times larger
94 than previously estimated by Bird et al. (2015). Fires occurring over the past few decades in the Amazon have
95 resulted in substantial effects on forest dynamics and structure (Barlow and Peres 2008). However, there is little
96 information about whether fire caused by climate variation and/or past human occupation in Amazon has had
97 substantial legacy effects on present-day forest structure, composition and functioning.

98 Hardesty et al. (2005) classified the Amazon region as a fire-sensitive ecosystem, which is damaged by
99 fire that disrupts ecological processes, kills many individuals, or even eliminates species that have not evolved
100 under this selective force. Undisturbed moist forest rarely burns (Uhl et al. 1998); however, forests that have
101 burned once are more likely to burn again (Cochrane et al. 1999). The widespread historical impact of humans
102 and fire on Amazonian forests is widely debated (McMichael et al. 2012) and remain entirely unaccounted in
103 many influential studies (McMichael et al. 2017). Thus, even if fires were not a frequent environmental filter in
104 these forests, they might have assembled species with a restricted range of functional traits related to fire in
105 current forests, as has occurred in savannas (Dantas et al. 2013), making the forests more resilient to recent
106 burning or to recent dry periods than previously thought. As a result of this environmental filter (fire), the
107 structure, species composition, and functional traits (any attribute that has potentially significant influence on
108 plant establishment, survival, and fitness: Reich et al. 2003) of forests of the Amazon Basin may have changed

109 dramatically with time. Thus, studying these traits is fundamental, as they can provide a mechanistic basis for
110 understanding how ecosystems function (Cadotte et al. 2015) and, specifically in this study, whether these traits
111 can potentially reveal how the Amazon Basin forest community relates to fire and climate.

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

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

133 Understanding the disturbance history in tropical forests is vitally important for interpreting their
134 present-day structure, composition and dynamics. One of the main drivers of past change in the Amazon biome
135 may have been fire (Pinter et al. 2011). Our study introduces a new important potential predictor to determine
136 plant traits distributions across the Amazon Basin, soil PyC abundance. An understanding of soil PyC
137 distribution may provide a large-scale perspective of fire history (Whitlock and Larsen 2001). Thus, our

138 objective in this study was to assess the relationships between vegetation traits and environmental filters,
139 accounting for climate and historical fires (PyC) across representative samples of the Amazon rain forest. We
140 hypothesized that, despite the Amazon biome being a fire-sensitive ecosystem, some functional traits persist in
141 modern old-growth rain forest vegetation as a legacy of past fire regimes. Specifically, we hypothesized that
142 functional traits representative of species growing in fire-prone environments, such as higher wood density and
143 shorter trees (Brando et al. 2012), are positively associated with soil PyC abundance and that functional traits
144 that respond to dry climate such as high numbers of dry fruit-type species and seasonal fruiting (Sfair et al. 2016)
145 are related to drier and hotter climate conditions.

146

147 MATERIAL AND METHODS

148 Forest sites

149 Species richness and individual abundance data-from 34 1-ha permanent forest plots across the range of
150 local and regional environmental gradients that occur in Amazonia were used in our analysis (Online Resource 1
151 and Figure 1). The forest data, including *Terra Firme* forests on both clay-rich and white-sand substrates, and
152 seasonally flooded forest are summarized in Appendix 1. Of these 34 plots, 33 are in the ForestPlots.net
153 database, a web repository for long-term tropical forest inventory plots, where trees ≥ 10 cm diameter within an
154 area are individually identified, measured and tracked through time (Lopez-Gonzalez et al. 2009, 2011), and one
155 is in the Tropical Ecology Assessment and Monitoring (TEAM) database (MPEG 2014, VEGCAX1). All sites
156 examined were old-growth humid forests, excluding Anthropogenic Dark Earth sites (*Terra Preta de Índio*).
157 Based on the vegetation and local information, there was no evidence of recent, major, direct human impact or
158 fire. The most abundant species in each plot (more than five individuals per plot) were chosen for analysis.

159

160 Plant traits

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

166 Seed type was extracted from several studies (mainly Amaral et al. 2009, Muniz 2008, Stefanello et al.
167 2009, Yamamoto et al. 2007). If a species could not be found in published studies, fruit type was drawn from
168 genus level information; it is well known that reproductive traits show clustering in phylogenetic trees (Chazdon
169 et al. 2003). All fruit morphologies of the genera were checked in books, manuscripts and published floras. We
170 estimated fruit size and leaf length and we assessed maximum plant height based on botanical registers at Lista
171 de Espécies da Flora do Brasil (<http://www.floradobrasil.jbrj.gov.br/>) and SpeciesLink Network
172 (<http://splink.cria.org.br/>). For these previous parameters, we used at least ten different plants, including rarer
173 individuals (smaller and bigger ones). If the differences between individuals were high, we expanded the sample
174 collection. Wood density was obtained from Forestplots.net database or, when the species was absent, from the
175 Wood Density database (Ketterings et al. 2001; [http://www.worldagroforestry.org/output/wood-density-](http://www.worldagroforestry.org/output/wood-density-database)
176 [database](http://www.worldagroforestry.org/output/wood-density-database)).

177 Fruiting phenology was assigned based on the months that the species were collected with fruits on
178 botanical registers at Lista de Espécies da Flora do Brasil (for species that were over-collected we selected the
179 months with highest numbers of exsiccatae). We could not relate collections to specific plot locations, thus we
180 treated plant registers of different sites as originating from the same location. Although the timing of seasonal
181 events, such as fruiting, is highly sensitive to climate (Chuine 2010) since collections cover a wide range of
182 dates, the data should represent general phenology patterns for most species. Two phenology traits were derived
183 from the survey: duration given by i) number of days - number of months that the species was recorded as
184 having fruit multiplied by 30 and ii) fruiting timing occurring in the dry and/or wet periods - dry period, if a
185 reproductive phenophase was registered between July and November it was said to be in the dry period
186 (seasonality defined according to Huete et al. 2006 in a multiple scale study including an extensive 2,000 km
187 climate transect through eastern and central Amazonia), wet period, if registered between December and June, or
188 both periods, if the phenophase was registered in mixed periods. The 34 studied plots include a wide geographic
189 range with different seasonality calendars (Girardin et al. 2016), from Guyana to Ecuador to the south border of
190 Amazonia in Mato Grosso state. These different calendars have different dry and wet periods, and it is
191 methodologically challenging to determine phenology including such site-specific variations. For this reason, we
192 chose only one dry and wet period for the whole Amazon region, defined according to the previously mentioned
193 study. Flowering phenology was not evaluated since it was found for less than half of all species.

194

195 Environmental variables

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

210

211 Data analyses

212 The relationships between species traits and environmental variables were tested by RLQ combined
213 with fourth corner analysis (Kleyer et al. 2012, Dray et al. 2014). This analysis aims to investigate the
214 relationships between two tables, R (environmental characteristics) and Q (species attributes, in our case), using
215 a third table, L (species abundance matrix), to establish the linkage and their combined ordination. R represents a
216 matrix whose rows are the sites and columns the environmental characteristics for each plot; Q represents a
217 matrix whose rows are tree species abundance and columns are the attributes for each species; L represents a
218 matrix whose rows are plots and whose columns are tree species. Each matrix was primarily analyzed in
219 isolation by means of a Principal Component Analysis (PCA) for environmental data and traits, and according to
220 a Correspondence Analysis (CA) for species abundance matrices. The relation among these matrices was
221 established by means of a CoInertia analysis to maximize their covariance.

222 We followed the new approach recommended by Dray et al. (2014) in applying the fourth-corner tests
223 to the output of the RLQ analysis, which allows for quantification and statistical testing of the relationships

224 between environmental variables and species traits by means of two null models. We used a combination of
225 model 2 – which tests for the links between the matrices L and Q, with the null hypothesis assuming that the
226 distribution of species with fixed (i.e. species-independent) traits is not influenced by environmental conditions,
227 jointly with the model 4 – which tests for the links between L and R, with the null hypothesis considering that
228 the species composition with fixed environmental conditions is not influenced by the species traits. According to
229 the aforementioned authors, this new approach combining these two permutation models has correct type I error
230 rates, but at the same time, as ter Braak et al (2016) stated it does not consider spatial, temporal and phylogenetic
231 autocorrelation. Significance of the relationship between species traits and environmental variables was assessed
232 based on 999 permutations. All analyses were performed using the *ade4* package for R v.3.2.1 (R-Development
233 Core Team 2013).

234

235 RESULTS

236 Our dataset represented 9789 individuals distributed across 378 species and the 34 old-growth forest
237 plots. Of this total, 173 species had few individuals (less than 10 individuals in only one or two plots). The ten
238 most common species (according to frequency in plots and abundance) were *Tetragastris altissima*
239 (*Burseraceae*), *Iriartea deltoidea* (*Arecaceae*), *Euterpe precatoria* (*Arecaceae*), *Pseudolmedia laevis* (*Moraceae*),
240 *Eschweilera coriacea* (*Lecythidaceae*), *Amaioua guianensis* (*Rubiaceae*), *Cheiloclinium cognatum*
241 (*Celastraceae*), *Socratea exorrhiza* (*Arecaceae*), *Rinorea guianensis* (*Violaceae*) and *Miconia pyrifolia*
242 (*Melastomataceae*).

243 Plant traits varied according to the sites (Table 1): fleshy fruit species were dominant in most sites with
244 two exceptions, ELD-01 and FMH-01, which were the more easterly sites (Venezuela and Guyana) (Figure 1).
245 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
246 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
247 staggered through the year.

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

252 traits (Table 2: Q table), respectively, indicating variability in species trait values across the environmental
253 gradient.

254 Among those traits, only the variability in diaspore type and wood density was explained by the
255 variability in the environmental gradient ($r=0.89$, $p=0.001$ and $r=-0.60$, $p=0.001$ respectively; Figure 2). And
256 among these environmental parameters, average temperature ($r=-0.85$, $p=0.001$), water deficit (MCWD) ($r=-$
257 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
258 the studied functional traits. There was also a significant association between PyC ($r=-0.71$, $p=0.001$) and
259 maximum temperature of the warmest month ($r=0.88$, $p=0.001$) with the second RLQ axis, but with traits
260 unrelated to this axis, which may indicate a lack of detectable effect of past fires on contemporary composition
261 and functioning of Amazon Basin forests (Figure 2).

262 We also found a significant relationship between species composition and environmental variables
263 (model 2, $p=0.007$) and between species composition and functional traits (model 4, $p=0.009$). These results
264 indicate that species composition is dependent on the environmental conditions (altitude, climate and fire-
265 history) of the sites and influenced by species' functional attributes.

266 Species with denser wood were associated with hotter ($r=0.28$, $p=0.002$) and lower elevation
267 environments ($r=-0.20$, $p=0.037$); species with dry diaspores were associated with drier ($r=0.23$, $p=0.007$), hotter
268 ($r=0.18$, $p=0.014$) and lower elevation environments ($r=-0.19$, $p=0.01$); the opposite was found for the
269 relationships between fleshy fruit species and MCWD ($r=-0.23$, $p=0.008$), temperature ($r=-0.18$, $p=0.017$) and
270 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
271 duration was shorter ($r=-0.17$, $p=0.027$) in sites where annual precipitation was higher (Figure 3). None of the
272 studied traits were significantly associated with PyC (Figure 3); however, the analyses showed a tendency for
273 less species fruiting in the dry period in plots with higher percentage soil PyC ($r=-0.12$, $p=0.091$; Figure 4).

274

275 DISCUSSION

276 Our results show that functional traits and environmental variables jointly predict variation in tree
277 species composition in the Amazon Basin. The findings of this study represent some of the main hyper-dominant
278 species that occur throughout the Amazon Basin (ter Steege et al. 2013) and dominant species in Cerrado-
279 Amazon forest transition sites (Ackerly et al. 1989, Marimon et al. 2006, Mews et al. 2011, Morandi et al. 2016).
280 The fourth-corner permutation models assessing the trait–environment-species link suggests that the distribution

281 of species with fixed traits is influenced by environmental characteristics and that the species composition of
282 sites with given environmental characteristics is influenced by species traits. Kraft et al. (2008), using a
283 functional ecology approach, also found evidence for niche-based processes in an Amazonian forest. Other
284 recent studies have shown that Amazonian tree species distribution respond strongly to environmental variation
285 (Esquivel-Muelbert et al. 2016) and the strength of response is significantly correlated to functional traits
286 (Rowland et al. 2014, Silva et al. 2014).

287 Differences in community structure and function were primarily driven by temperature and water
288 availability (and altitude, variable usually correlated to the other two climate parameters: Benavides et al. 2016).
289 Therefore, functional traits representative of fire-prone environment species such as higher wood density and
290 shorter trees were not associated with soil PyC abundance. These results of no detectable legacy of fire effect on
291 plant traits may be a consequence of several factors: i) historical fires may have been locally and/or temporally
292 restricted and not associated with a widespread and/or frequent fire regime; therefore, impacts on biodiversity
293 would have been small and/or heterogeneous,; ii) alternatively, sufficient time may have passed since the last fire
294 (hundreds of years) to allow the forest to recover; iii) soil pyrogenic carbon storage may not be a suitable
295 predictor of past-fires. Despite these factors, the significant relation between PyC and the second RLQ axis and
296 marginal significance with one of the studied traits, suggests that more aspects of past fire events need to be
297 investigated. Large-scale carbon radiocarbon dating, although cost prohibitive, would provide key information
298 about time since last fire.

299 It has been shown that fire strongly mediated the effect of other environmental variables on some traits
300 in a longleaf pine savanna in California, indicating that strong environmental gradients cannot be considered
301 independently when assessing their effects on functional traits (Ames et al. 2015). However, savannas are fire
302 prone ecosystems, which evolved as a response of fire regimes, i.e. intensity, duration and frequency of burnings
303 (Bowman et al. 2009). In tropical rain forests such as our study, though, the data from charcoal radiocarbon
304 dating imply a fire return of hundreds or thousands of years (Sanford et al. 1985, Turcq et al. 1998), with distinct
305 spatial and temporal patterns (Bush et al. 2007, Bush et al. 2008). Some preliminary charcoal dating results of
306 three studied plots may confirm return times and spatial patterns: an eastern Amazonia plot had fire estimates of
307 1134 years before present (BP) (charcoal in 10-20 cm) and 1620 yr BP (30-50 cm); a northern Amazonia plot,
308 989 yr BP (32 cm); and a south edge plot a range of 96 yr BP (10-20 cm), 806 yr BP (20-30 cm) and 1372 yr BP
309 (150-200 cm). Other recent AMS results from the same region show a larger return interval in fire records for

310 some sites, ~6,000 years (from 6876 to 365 yr BP: Goulart et al. 2017). Previous studies of soil charcoal have
311 also shown a spatially localized and heterogeneous signature of fire on Amazon forests (McMichael et al. 2012,
312 McMichael et al. 2017).

313 Thus, rather than a pristine tropical forest, some areas in the Amazon Basin have been interpreted as
314 constructed landscapes, dramatically altered by past indigenous groups (Erickson 2008, Heckenberger et al.
315 2007, Roosevelt 2003) indicating propensity for regional forests to burn, especially during periods of drought
316 (Bush et al. 2008). Anthropogenic fire has been a factor in shaping plant communities through human prehistory,
317 e.g., generally a woody non-fire-prone vegetation type tends to transition to a more herbaceous, flammable and
318 shade-intolerant vegetation type with frequent fire (Pinter et al. 2011), changing forest composition (Barlow and
319 Peres 2008) and structure (Bennett et al. 2013) and species abundance (Piperno and Becker 1996, depending on
320 the regional pool of species: Mittelbach & Schemske 2015). Brando et al. (2014) presented the first evidence of
321 substantial fire-induced tree mortality due to altered fire regimes and a widespread invasion by flammable
322 grasses in a southern Amazonian forest subjected to experimental repeat burns. Besides fire-induced mortality,
323 other demographic patterns also play important roles after a disturbance such as recruitment and growth of
324 individuals. For these reasons, forest recovery is very slow (Almeida et al. 2016, Barlow and Peres 2008, Flores
325 et al. 2012, Uhl et al. 1998). However, recovery may be fast enough to erase the signal of fire history on the
326 functional composition of this vegetation, considering the limited reported charcoal AMS dated fire
327 spatiotemporal patterns with long times since last fire in old-growth forests. In fact, it may take only a decade for
328 trait changes to be apparent at the individual level as a response to some stress, as van der Sande et al. (2016)
329 found for wood density and specific leaf area in Neotropical forests subject to increased drought stress.

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

336 Lowland Amazon tropical rain forests possess an annual climate that is warm with little temperature
337 variation; rainfall, however, varies spatially and is highly seasonal in some regions: the south and southeast are
338 drier and more seasonal, while the west and northwest are wetter and aseasonal (Sombroek 2001). During the

339 last century the Amazon warmed by 1°C, but rainfall pattern changes are more difficult to identify (IPCC 2013).
340 Climate change is viewed as a threat to biodiversity (Bellard et al. 2012). Despite some resilience to moderate
341 annual and repeat droughts (Davidson et al. 2012, Feldpausch et al. 2016), plant traits related to drought-induced
342 mortality, such as lower wood density, larger tree size, fast growing pioneers and evergreens (Feldpausch et al.
343 2016, O'Brien et al. 2017, Phillips et al. 2009) may be not be advantageous in drier sites, thus, highlighting the
344 need to identify traits that account for differential tree vulnerability to environmental stress.

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

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

365 Five out of the seven functional traits evaluated across all 378 species were correlated with some
366 environmental variable, indicating that the selected traits and the independent parameters were adequate in that
367 they cover the range of traits commonly deemed essential to woody plant strategy (Pausas and Lavorel 2003).

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

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

384 The long-term ecological consequences of fire in Amazon forests are not clear. Fires are rapidly
385 becoming a common occurrence in vast areas of both disturbed and undisturbed Amazonian forests and
386 pyrogenic carbon analysis indicates fire historically occurred in all our plots, including even the wettest plots of
387 northwestern Amazonia, but the time-scale of these burnings seems to be longer than that the needed for forest
388 functional composition recovery. In this study, we observed that functional traits and environmental variables
389 jointly predicted variations in tree species composition in Amazon Basin forests. We also showed the lack of a
390 detectable effect of PyC on specific traits, but the existence of a secondary association with the general traits
391 distribution (axis 2) indicates that the consideration of climatic variables alone may not be sufficient to explain
392 species distributions and the maintenance of diversity and functioning in Amazonian forests. The future
393 trajectory of Amazonian forests that experience drought and fire will depend, in part, upon tree species
394 composition and drought- and fire-tolerance traits, both of which still need to be better disentangled and
395 understood.

396

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602 Table 1. Vegetation trait descriptions of 34 forest plots in Amazonia. (Abbreviations: unk, unknown; Jan,
603 January.... Dec, December; d: dry period; w: wet period).

| 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 | 3.2 | Oct, Feb d,w |
| AGP-02 | 11/100 | 17 | 24 | 0.56 | 1 unk 4 dry 6 fleshy | 3.4 | Feb w |
| ALF-02 | 22/430 | 13 | 24 | 0.61 | 1 unk 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 |

| | | | | | | | |
|---------|--------|----|----|------|-----------------------|-----|-------------|
| LFB-01 | 20/460 | 14 | 21 | 0.58 | fleshy 5 dry 15 | 2.7 | Oct d |
| LFB-02 | 18/435 | 15 | 21 | 0.55 | fleshy 5 dry 13 | 3.2 | Oct d |
| NOU-06 | 7/89 | 17 | 27 | 0.64 | fleshy 1 dry 6 | 2.9 | Oct,Jan d,w |
| POR-01 | 25/293 | 14 | 22 | 0.62 | fleshy 5 dry 20 | 2.9 | Oct d |
| POR-02 | 23/270 | 12 | 22 | 0.64 | fleshy 4 dry 19 | 3.1 | Aug-Oct d |
| RST-01 | 12/195 | 13 | 19 | 0.50 | fleshy 1 dry 11 | 7.0 | Jul-Aug d |
| SCR-05 | 30/460 | 12 | 25 | 0.71 | fleshy 7 dry 23 | 5.2 | Jan w |
| SUC-02 | 19/164 | 15 | 21 | 0.62 | fleshy 5 dry 14 | 4.2 | Oct d |
| TAM-05 | 28/317 | 13 | 23 | 0.60 | fleshy 5 dry 23 | 2.8 | Oct d |
| TAN-04 | 21/509 | 12 | 19 | 0.63 | fleshy 3 dry 18 | 2.1 | Apr-May w |
| TEC-01* | 19/214 | 11 | 25 | 0.78 | fleshy 6 dry 13 | 2.9 | Nov d |
| VCR-02 | 19/560 | 11 | 19 | 0.66 | fleshy 2 dry 17 | 2.9 | Sep d |
| YAN-01 | 19/225 | 22 | 26 | 0.56 | fleshy 7 dry 12 | 4.8 | Oct d |

605 Table 2. Results of RLQ analysis using environmental variables and species traits. (a) Eigenvalues (and % of
606 total co-inertia) for the first two axes. Ordinations of tables R (principal components analysis – PCA), L
607 (correspondence analysis – CA) and Q (PCA). (b) Summary of RLQ analysis: eigenvalues and percentage of
608 total co-inertia accounted for by the first two RLQ axes, covariance and correlation (and % variance) with the
609 correspondence analysis of the L matrix and projected variance (and % variance) with the R and Q matrices.

| | 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) |

610

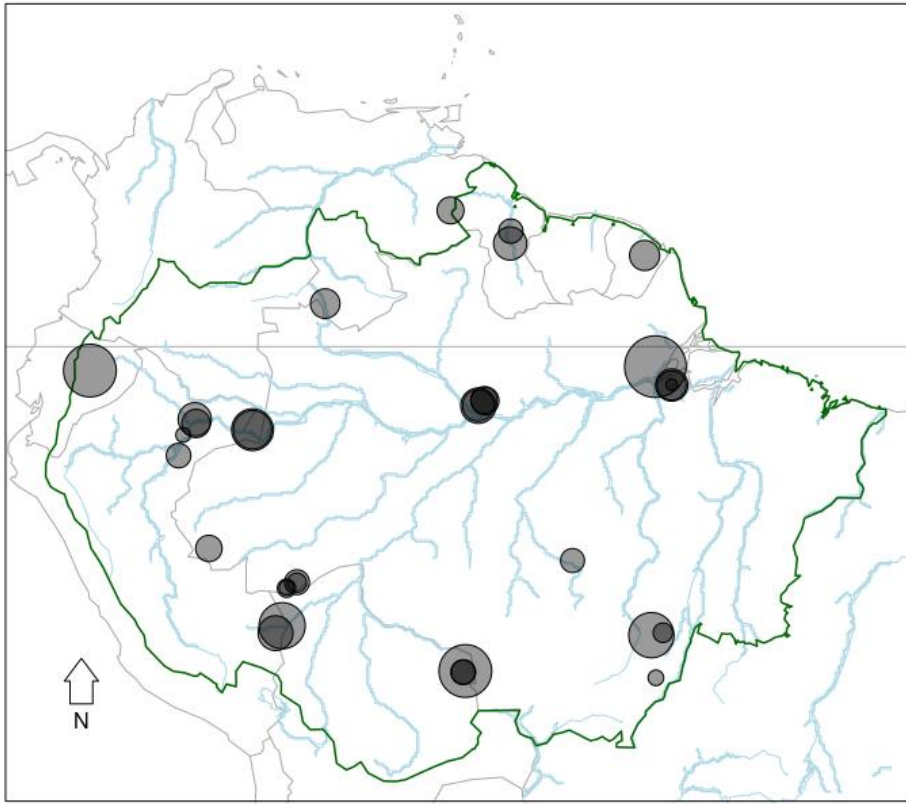
611 Figure 1. Location of the Amazonian study sites (circles) showing the variation in percentage pyrogenic carbon
612 in total soil. The green outline shows Amazonia boundary, blue lines are the rivers and streams. Circles are
613 proportional to the percentage pyrogenic carbon in soil samples (0-30cm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

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

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

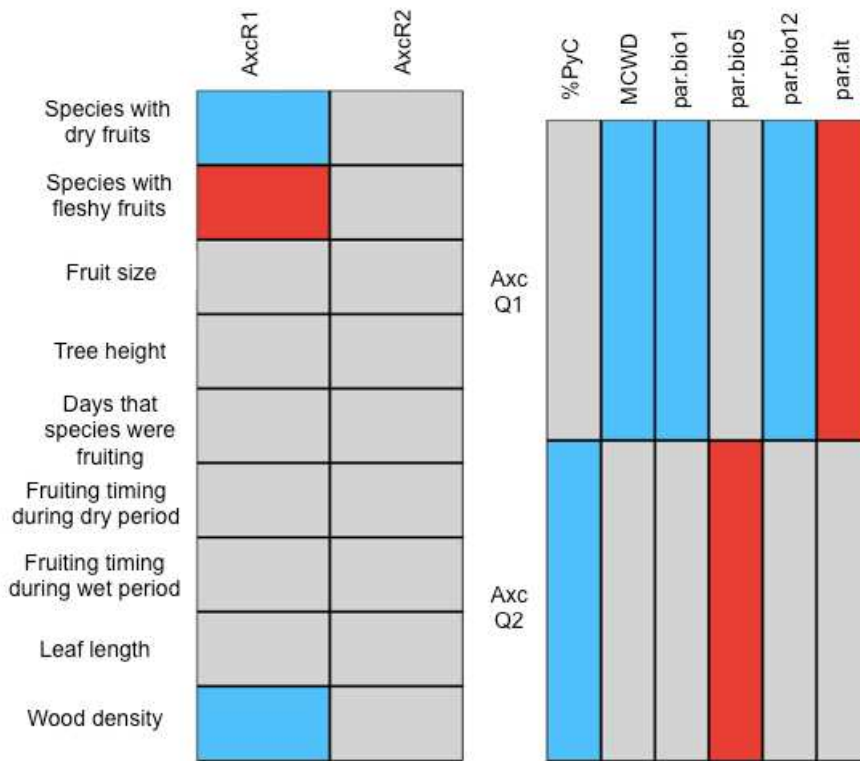
626 Figure 4. Percentage of species fruiting during dry period plotted against percentage pyrogenic carbon in total
627 soil.

628



629
630 Figure 1.
631

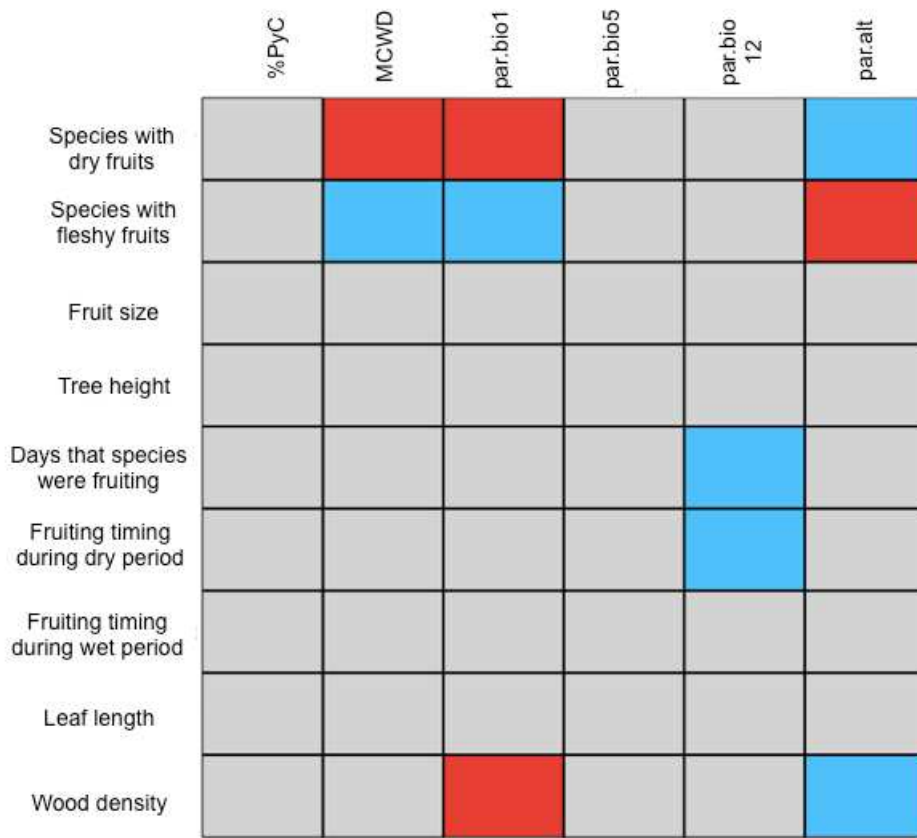
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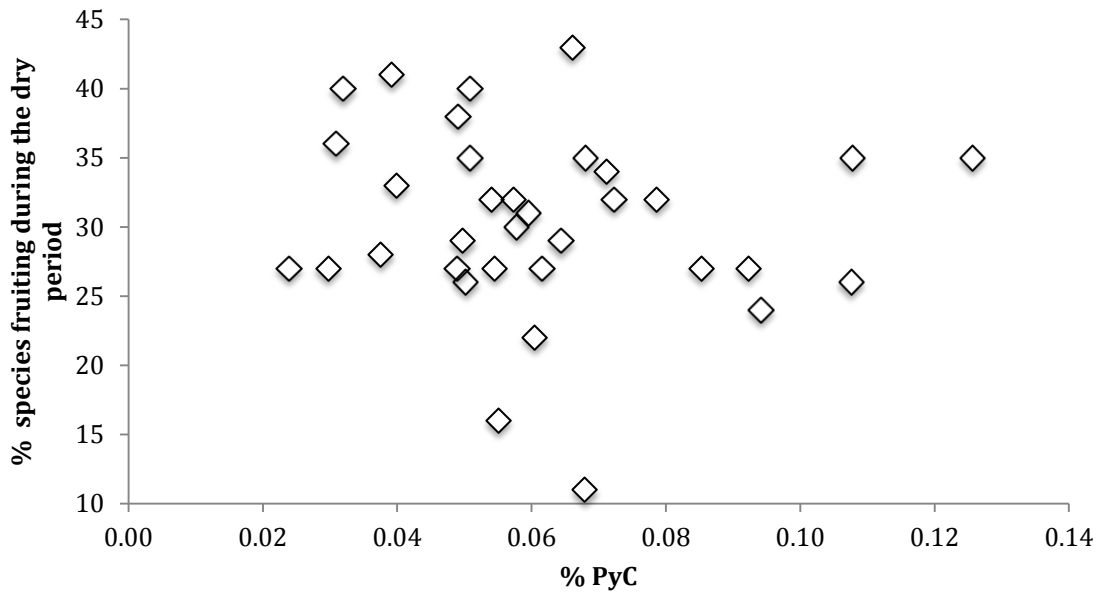
634 Figure 2.

635



636

637 Figure 3.



638

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

641

642 Online Resource 1. Site descriptions of 34 forest plots in the Amazon Basin.

| Name | Plot Code | Country | Latitude | Longitude | Forest type | Year of census |
|--|-----------|---------------|----------|-----------|-------------------------|----------------|
| Amacayacu: Agua Pudre E | AGP-01 | Colombia | -3.72 | -70.30 | terra firme | 2011 |
| Amacayacu: Agua Pudre U | AGP-02 | Colombia | -3.72 | -70.30 | terra firme | 2006 |
| Parque Cristalino, Alta Floresta, MT | ALF-02 | Brazil | -9.58 | -55.92 | terra firme | 2008 |
| Allpahuayo C | ALP-30 | Peru | -3.95 | -73.43 | white sand forest | 2011 |
| BDFFP, 1101 Gaviao | BDF-03 | Brazil | -2.42 | -59.85 | terra firme | 2009 |
| BDFFP, 1109 Gaviao | BDF-08 | Brazil | -2.40 | -59.90 | terra firme | 2009 |
| Bionte 2 | BNT-02 | Brazil | -2.64 | -60.15 | terra firme | 2010 |
| Bionte 4 | BNT-04 | Brazil | -2.63 | -60.15 | terra firme | 2010 |
| Caxiuna 1 | CAX-01 | Brazil | -1.74 | -51.46 | terra firme | 2009 |
| Caxiuna 6 | CAX-06 | Brazil | -1.72 | -51.46 | terra firme | 2009 |
| Cuzco Amazonico, CUZAM1E | CUZ-01 | Peru | -12.54 | -69.06 | terra firme, floodplain | 2008 |
| RESEX Chico Mendes: Seringal Dois Irmãos 1 | DOI-01 | Brazil | -10.57 | -68.32 | terra firme | 2009 |
| RESEX Chico Mendes: Seringal Dois Irmãos 2 | DOI-02 | Brazil | -10.55 | -68.31 | terra firme, bamboo | 2009 |
| El Dorado, km93, plotG1, ED1 | ELD-01 | Venezuela | 6.11 | -61.41 | terra firme | 2009 |
| Fazenda Floresta, Ribeirão Cascalheira, MT | FLO-01 | Brazil | -12.81 | -51.34 | terra firme | 2013 |
| Forest reserve Mabura hill 01 | FMH-01 | Guyana | 5.17 | -58.69 | terra firme | 2010 |
| Huanchaca Dos, plot 1 | HCC-21 | Bolivia | -14.56 | -60.75 | terra firme | 2009 |
| Iwokrama 22 | IWO-22 | Guyana | 4.62 | -58.72 | terra firme | 2010 |
| Jatun Sacha 2 | JAS-02 | Ecuador | -1.07 | -77.62 | terra firme | 2010 |
| Jenaro Herrera A Terraza Alta | JEN-11 | Peru | -4.88 | -73.63 | terra firme | 2011 |
| Jari 1 | JRI-01 | Brazil | -1.00 | -52.05 | terra firme | 1996 |
| Los Fierros Bosque I | LFB-01 | Bolivia | -14.58 | -60.83 | terra firme | 2009 |
| Los Fierros Bosque II | LFB-02 | Bolivia | -14.58 | -60.83 | terra firme | 2009 |
| Nourages | NOU-06 | French Guyana | 4.08 | -52.68 | | 2012 |
| RESEX Chico Mendes: Seringal Porongaba 1 | POR-01 | Brazil | -10.82 | -68.77 | terra firme | 2009 |
| RESEX Chico Mendes: Seringal Porongaba 2 | POR-02 | Brazil | -10.80 | -68.77 | terra firme | 2009 |
| Base da Restauração - Reserva Extrativista do Alto Juruá | RST-01 | Brazil | -9.04 | -72.27 | terra firme | 2009 |
| San Carlos de Rio | SCR-05 | Venezuela | 1.93 | -67.04 | terra firme | 2012 |

| | | | | | | |
|------------------------------------|--------|--------|--------|--------|-------------|------|
| Negro, MAB site, Yevaro, plot B | | | | | | |
| Sucusari B | SUC-02 | Peru | -3.25 | -72.90 | terra firme | 2012 |
| Tambopata plot 3 | TAM-05 | Peru | -12.83 | -62.97 | terra firme | 2008 |
| Fazenda Tanguro, Querência, MT | TAN-04 | Brazil | -12.92 | -52.37 | terra firme | 2008 |
| Team Caxiuanã 1 * | TEC-01 | Brazil | -1.71 | -51.46 | terra firme | 2014 |
| Fazenda Vera Cruz, plot 2 | VCR-02 | Brazil | -14.83 | -52.17 | terra firme | 2008 |
| Yanamono A | YAN-01 | Peru | -3.43 | -72.84 | terra firme | 2011 |

643 *data from the TEAM network plot; all other data from the RAINFOR network.

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