

# Litter inputs and standing stocks in riparian zones and streams under secondary forest and managed and abandoned cocoa agroforestry systems

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**Background.** Cocoa is an important tropical tree crop that is mainly cultivated in agroforestry systems (AFS). This system, known as cabruca in northeastern Brazil, holds promise to reconcile biodiversity conservation and economic development. However, since cocoa AFS alters forest structure composition, it can affect litter dynamics in riparian zones and streams. Thus, our objective was to determine litter inputs and standing stocks in riparian zones and streams under three types of forest: managed cocoa AFS, abandoned cocoa AFS, and secondary forest. **Methods.** We determined terrestrial litter fall (TI), vertical (VI) and lateral (LI) litter inputs to streams, and litter standing stocks on streambeds (BS) in the Atlantic Forest of northeastern Brazil. Litter was collected every 30 days from August 2018 to July 2019 using custom-made traps. The litter was dried, separated into four fractions (leaves, branches, reproductive organs, and miscellaneous material) and weighed. **Results.** Terrestrial litter fall was similar in all forests, ranging from 89 g m<sup>-2</sup> month<sup>-1</sup> in secondary forest (SF) to 96 g m<sup>-2</sup> month<sup>-1</sup> in abandoned cocoa AFS (AC). Vertical input were higher in AC (82 g m<sup>-2</sup> month<sup>-1</sup>) and MC (69 g m<sup>-2</sup> month<sup>-1</sup>) than in SF (40 g m<sup>-2</sup> month<sup>-1</sup>), whereas lateral input were higher in MC (43 g m<sup>-2</sup> month<sup>-1</sup>) than in AC (15 g m<sup>-2</sup> month<sup>-1</sup>) and SF (24 g m<sup>-2</sup> month<sup>-1</sup>). Standing stocks followed the order SF>AC>MC, corresponding to 425, 299 and 152 g m<sup>-2</sup>. Leaves contributed most to all litter fractions in all forests. Reproductive plant parts accounted for a larger proportion in managed AFS. Branches and miscellaneous litter were also similar in all forests, except for higher benthic standing stocks of miscellaneous litter in the SF. Despite differences in the

amounts of litter inputs and standing stocks among the forests, seasonal patterns in the abandoned AFS (AC) were more similar to those of the secondary forest (SF) than the managed AFS, suggesting potential of abandoned AFS to restore litter dynamics resembling those of secondary forests.

1 **Litter inputs and standing stocks in riparian zones and streams under secondary**  
2 **forest and managed and abandoned cocoa agroforestry systems**

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25 **Abstract**

26 **Background.** Cocoa is an important tropical tree crop that is mainly cultivated in agroforestry  
27 systems (AFS). This system, known as *cabruca* in northeastern Brazil, holds promise to  
28 reconcile biodiversity conservation and economic development. However, since cocoa AFS  
29 alters forest structure composition, it can affect litter dynamics in riparian zones and streams.  
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35 Brazil. Litter was collected every 30 days from August 2018 to July 2019 using custom-made  
36 traps. The litter was dried, separated into four fractions (leaves, branches, reproductive organs,  
37 and miscellaneous material) and weighed.

38 **Results.** Terrestrial litter fall was similar in all forests, ranging from  $89 \text{ g m}^{-2}\text{month}^{-1}$  in  
39 secondary forest (SF) to  $96 \text{ g m}^{-2} \text{ month}^{-1}$  in abandoned cocoa AFS (AC). Vertical input were  
40 higher in AC ( $82 \text{ g m}^{-2} \text{ month}^{-1}$ ) and MC ( $69 \text{ g m}^{-2} \text{ month}^{-1}$ ) than in SF ( $40 \text{ g m}^{-2} \text{ month}^{-1}$ ),  
41 whereas lateral input were higher in MC ( $43 \text{ g m}^{-2} \text{ month}^{-1}$ ) than in AC ( $15 \text{ g m}^{-2} \text{ month}^{-1}$ ) and  
42 SF ( $24 \text{ g m}^{-2} \text{ month}^{-1}$ ). Standing stocks followed the order SF>AC>MC, corresponding to 425,  
43 299 and  $152 \text{ g m}^{-2}$ . Leaves contributed most to all litter fractions in all forests. Reproductive  
44 plant parts accounted for a larger proportion in managed AFS. Branches and miscellaneous litter  
45 were also similar in all forests, except for higher benthic standing stocks of miscellaneous litter  
46 in the SF. Despite differences in the amounts of litter inputs and standing stocks among the  
47 forests, seasonal patterns in the abandoned AFS (AC) were more similar to those of the

- 48 secondary forest (SF) than the managed AFS, suggesting potential of abandoned AFS to restore  
49 litter dynamics resembling those of secondary forests.

## 50 Introduction

51 Riparian zones are important for the functioning of headwater streams (Vannote et al., 1980;  
52 Naiman, Décamps & McClain, 2005), including in tropical zones (Gonçalves Júnior et al., 2014;  
53 Bambi et al., 2016; Rezende et al., 2017a; Rezende et al., 2019; Calderón et al., 2019). The  
54 riparian canopy limits instream primary production and provides allochthonous organic matter to  
55 stream and riparian food webs in the form of litter, which increases heterotrophic metabolism  
56 (Gonçalves Júnior et al., 2014; Rezende et al., 2019). Therefore, litter dynamics are a  
57 fundamental characteristic of headwater streams (Abelho & Graça, 1996; Neres-Lima et al.,  
58 2017). In the tropics, litter is typically supplied throughout the year (Tonin et al., 2017), although  
59 this pattern varies among forest types (Lindman et al., 2017; Seena et al., 2017), largely driven  
60 by precipitation and temperature regimes (Bambi et al., 2016; Tonin et al., 2017). Changes in the  
61 structure and composition of riparian forests can affect the supply of litter to streams and their  
62 riparian zones (DeLong & Brusven, 1994; Ferreira et al., 2019; Wild, Gücker & Brauns, 2019), as  
63 well as in-stream litter dynamics (Stufin, Wohl & Dwire, 2016; Tiegs et al., 2019).

64 Many tropical forests are jeopardized by rapid deforestation and expansion of agriculture (Bawa  
65 et al., 2004). This includes the Atlantic Forest of Brazil as one of the most threatened tropical  
66 forests worldwide (Winbourne et al., 2018; Taubert et al., 2018). Agroforestry systems (AFSs),  
67 however, have potential to partly reconcile the conservation of tropical forest patches with  
68 economic development (Cassano et al., 2009; Schroth et al., 2011). One example is the  
69 cultivation of cocoa in the Atlantic Forest of northeast Brazil where cocoa trees (*Theobroma*  
70 *cacao* L.) are grown in AFS that cover a large portion of the remnant Atlantic Forest (Piasentin  
71 et al., 2014). The cocoa trees are planted in the shade of native forest trees (dominant and  
72 codominant strata) and are surrounded by natural vegetation. Therefore, cocoa AFS are thought

73 to cause less environmental impact than other crop systems (Johns, 1999; Sambuichi, 2002), with  
74 benefits for local biodiversity (Faria et al., 2007; Cassano et al., 2009; Schroth et al., 2011).  
75 Important processes such as the incorporation of large amounts of organic matter into the forest  
76 soil are indeed maintained in cocoa AFS (Beer et al., 1998; Gama-Rodrigues et al., 2010; Barreto  
77 et al., 2011; Fontes et al., 2014; Costa et al., 2018). Nevertheless, changes in the vegetation  
78 structure of AFS compared to unmanaged forest may affect the amount of litter deposited in  
79 riparian zones (DeLong & Brusven, 1994; Wild, Gücker & Brauns, 2019) and supplied to streams  
80 (Gonçalves Júnior et al., 2014).

81 Studies on litter dynamics in tropical streams and their riparian zones are scarce, especially under  
82 cocoa AFS, although some evidence suggests that replacing cocoa AFS changes the cycling of  
83 carbon and nitrogen in streams (Costa et al., 2017; Souza et al., 2017; Costa et al., 2018),  
84 possibly as a result of altered litter supply by riparian vegetation. Thus, the current study aimed  
85 to assess the influence of cocoa AFS on litter dynamics by determining differences in secondary  
86 forest and managed and abandoned AFS on litter inputs and benthic standing stocks in streams  
87 and riparian zones in these forests. We expected that i) managed and abandoned cocoa AFS  
88 produce more litter than secondary forest where forest structure (Curvelo et al., 2009; Dawoe,  
89 Isaac & Quashie-Sam, 2010; Fontes et al., 2014) and soil carbon stocks differ (Gama-Rodrigues  
90 et al. 2010, Costa et al. 2018) and nutrients are rapid cycled (Nair et al. 1999); ii) streams  
91 running through forests with high litter production tend to receive larger amounts of litter  
92 (França et al., 2009; Gonçalves Júnior et al., 2014), resulting in greater litter standings stocks in  
93 the streambeds (Webster et al., 1994; Lisboa et al., 2015); and iii) seasonal patterns of litter  
94 inputs and standing stocks reflect precipitation patterns because water availability controls litter  
95 production (Tonin et al., 2017).

96

97 **Methods**98 *Study area*

99 The study was conducted in the riparian zones of three small watersheds (Fig. 1) representing  
100 secondary forest (E 485415, N 8397615), abandoned cocoa AFS (E 481551, N 8364478), and  
101 managed cocoa AFS (E 448466, N 8363187). All sites are located in the Atlantic Forest of  
102 southern Bahia in northeast Brazil. The climate is wet tropical (hot and humid with no defined  
103 dry season, Af according to the Köppen classification) with annual rainfall ranging from 1100 to  
104 2200 mm. The study streams are second-order according to the Strahler classification. Daily  
105 rainfall data were obtained from the website of the Real-Time Climate Monitoring Program of  
106 the Northeast Region (PROCLIMA; <http://proclima.cptec.inpe.br>) for the municipalities of  
107 Itacaré, Ilhéus, and Barro Preto (Fig. 2).

108 The secondary forest, which covers 9,275 ha, is located in a conservation area (Serra do Conduru  
109 State Park - License 2017-013654/TEC/PESQ-0014) (Martini et al., 2007). The vegetation is a  
110 mosaic of different developmental stages, including secondary forest and remnants of mature  
111 forests with different degrees of selective logging in the past (Winbourne et al., 2018). The  
112 uniform canopy of the forest exceeds 25 m in height and includes a few emerging individual  
113 trees, epiphytes, large lianas, and a dense understory (Martini et al., 2007; Costa et al., 2018).  
114 Tree species density levels in the area were high at all sites, independent of forest successional  
115 stage; old growth forest totaled 144 species, old logged forest had 137 species, and recently  
116 logged forest 134. Of the species recorded in the Serra do Conduru State Park, 51.4% are  
117 endemic to the Atlantic Forest and 26% occur only in the south of Bahia (Martini et al., 2007).  
118 The abandoned AFS covers 73.4 ha and is located in an AFS (Santa Cruz) where crop

119 management was abandoned 20 years before the present study. Old cocoa trees and other,  
120 irregularly distributed species such as jackfruit, erythrina, embaúba, and jequitibá trees (Argôlo,  
121 2009) resulted in a medium level of shading (70%). The managed AFS is located in another AFS  
122 (Nova Harmonia) with a total area of 89.8 ha. It comprises areas under cocoa production, a forest  
123 patch in the central portion, and two areas undergoing regeneration (Santos et al., 2016).  
124 Management consists of pruning cocoa trees every six months, with the biomass left in place  
125 (Costa et al., 2018), complemented by vegetation cutting, and some liming for soil amelioration.  
126 The cocoa plants were spaced at 3x3m and intercropped with introduced shade trees (erythrina),  
127 according to the proposed management for the area.

### 128 *Litter inputs and benthic standing stocks*

129 Litter inputs and benthic standing stocks were determined from August 2018 to July 2019.  
130 Details of the methodology are described in Gonçalves Júnior et al. (2014) and Bambi et al.  
131 (2016). Terrestrial litter fall (TI), vertical (VI) and lateral (LI) litter inputs to streams, and litter  
132 deposited on the streambeds (benthic standing stock – BS) were assessed along 100 m stream  
133 stretches at each location (Figure 3).  
134 TI deposited on the riparian soil represents the amount of litter that can potentially be transported  
135 to the stream. It was collected with 10 nets (1 mm mesh, 2.5 m<sup>2</sup> total area), five on both sides of  
136 the streams, installed 1 m above the ground at 20 m distance from one another in the riparian  
137 zone. VI represents litter that falls directly into the streams from the riparian canopy. It was  
138 collected with 27 buckets (30 cm diameter, 1.9 m<sup>2</sup> total area) fixed to trees, perpendicular to the  
139 stream channel at a height of approximately 2 m. The buckets were arranged in three groups of  
140 nine, spaced approximately 30 m apart with a distance of 1 m between the individual buckets.  
141 Small holes in the bottom of the buckets allowed any collected water to drain. LI represents the

142 indirect input of litter by lateral movement from the forest floor to the stream due to gravity,  
143 runoff, wind, or animal action. LI was collected with 10 nets (1 mm mesh, 0.5 m length, 1.5 m<sup>2</sup>  
144 total area) arranged at ground level along the stream margins, five on both sides of the streams.  
145 Total litter input to the streams was calculated as the sum of lateral and vertical inputs. Finally,  
146 benthic standing stocks represent the litter accumulated on the streambed. It was estimated by  
147 taking Surber samples (0.25 mm mesh, 0.45 m<sup>2</sup> total area), five in each stream at 20 m distance  
148 from one another (Fig. 3).

149 The litter trapped in the nets and buckets was collected at monthly intervals and sorted into four  
150 fractions upon return to the laboratory: leaves, branches (i.e. woody pieces less than 25 cm in  
151 length), reproductive organs such as flowers and fruits, and miscellaneous material (i.e.  
152 unidentified plant matter and animal remains). The sorted litter was dried in an oven at 60 °C for  
153 72 hours and weighed. TI, VI and LI were expressed in g dry mass m<sup>-2</sup> d<sup>-1</sup>, LI per m<sup>2</sup> was  
154 calculated by dividing the collected litter mass by the trap width and multiplying the result by  
155 two (to account for inputs from both stream banks) and by the mean channel width (Pozo et al.,  
156 2009). The annual litter inputs to the streams and riparian zones corresponds to the sum of the  
157 mean monthly litter inputs during the study year (Table 1).

158

### 159 *Statistical analysis*

160 Differences among the forests in litter inputs and benthic standing stocks were assessed by  
161 generalized linear mixed-effects models (*glmer* function in the *lme4* package of *R*) with forest  
162 type (= site), time and the interaction of forest type and time as predictive variables (Bates et al.,  
163 2015). We considered trap and time as random factors to account for the pseudoreplicated design  
164 of the study, since the three forest types were represented only by a single site each. Separate

165 models were run for each of the plant organic matter fractions (leaves, branches, reproductive  
166 organs, miscellaneous material). P-values were obtained by likelihood ratio tests (chi-square  
167 distribution) of the full model against a partial model without the explanatory variable. All  
168 models were tested for error distribution by using the *hnp* package and function in *R*, and  
169 corrected for over- or underdispersion. Differences in litter inputs and standing stocks among  
170 forest types (sites) were also assessed by using bootstrapped 95% confidence intervals, which  
171 were computed by the bias-corrected and accelerated (BCa) method using the *boot* package and  
172 function in *R*, based on 1,000 bootstrap replicates (Davison & Hinkley, 1997; Canty & Ripley,  
173 2016). Differences were considered statistically significant when the bootstrapped confidence  
174 intervals did not overlap.

175 Given their flexibility, generalized additive mixed models (GAMM) were used as an additional  
176 approach to explore the seasonal patterns of litter inputs (i.e. vertical, lateral and terrestrial  
177 inputs) and standing stocks (Tonin et al., 2017; 2019). The input of leaves, branches,  
178 reproductive matter, or miscellaneous material over the 12-months study period was used as a  
179 normally distributed (identity-link function) predictor, nested within sites, as a random  
180 component of the GAMM models. Trap and time were used as random factors in the GAMM  
181 models. The degree of smoothing in an additive model is expressed as effective degrees of  
182 freedom (edf). Higher edf values indicate a lower degree of linearity (i.e. here variation over  
183 time), with a value of 1 indicating a perfectly linear effect. The additive mixed models were  
184 fitted by using the *by* command in the *mgcv* package in *R*. Validation was used to estimate the  
185 optimal degree of smoothing (Wood, 2017). The residual spread within models among sampling  
186 dates was measured by using the *varIdent* function in *R*.

187

**188 Results**

189 Leaf material was the single largest litter fraction, with percentages >60% for TI and VI and  
190 >70% for LI in the secondary forest and abandoned AFS (Fig. 4, Table 1). In the managed AFS,  
191 the percentages of TI, VI, and LI were 56, 41, and 65%, respectively. Leaves also represented  
192 large portions of the instream standing stock of litter, 61% in the abandoned AFS, 60% in the  
193 managed AFS, and 36% in the secondary forest. Miscellaneous types of organic matter was the  
194 second most abundant litter fraction of TI and VI observed in secondary forest and abandoned  
195 AFS (23% and 15% for TI and VI). Miscellaneous litter accounted for 43% of the standing stock  
196 in the secondary forest (Table 1). Branches were also a large portion of the litter standing stock  
197 in secondary forest (13%) and abandoned AFS (7%) (Table 1). Because of their sporadic and  
198 transient occurrence, reproductive parts were a low proportion of the total litter, except in  
199 managed AFS (Table 1), where they accounted for a higher proportion in all types of litter inputs  
200 and standing stocks (Fig. 4c,h,m,r). Branches and miscellaneous litter were generally similar in  
201 all forests, except for higher benthic standing stocks of miscellaneous litter in the secondary  
202 forest (Fig. 4).

203 The greatest seasonal variation in litter inputs and standing stocks was found for leaves, with the  
204 highest contributions during the transition between dry and rainy months and two seasonal peaks  
205 in some cases (Fig. 5a,c). Seasonal variation was less pronounced and generally not significant  
206 for branches, reproductive plant parts, and miscellaneous litter (Figs S1 to S3). Vertical litter  
207 inputs showed seasonal patterns for leaves in the secondary forest (effective degrees of freedom  
208 – edf = 5.5; Fig. 5d and abandoned AFS (edf = 5.1; Fig. 5e), with higher contributions during the  
209 rainy months, from November to February, in both SF and AC. In managed AFS, the  
210 contribution of leaves decreased linearly over time, as reflected by an edf value close to 1 (Fig.

211 5f). Terrestrial leaf inputs showed a sinusoidal pattern in the secondary forest (Fig. 5a) and  
212 managed AFS (Fig. 5c), which was reflected by high edf values of 7.0 and 6.7, respectively. A  
213 peak in the rainiest months was observed in all three forests but the second peak was missing in  
214 the abandoned AFS (Fig. 5b). The largest lateral inputs of leaves in managed AFS were observed  
215 from January to March (edf = 1.9; Fig. 5f), the period of least rainfall (Fig. 2). Standing stocks of  
216 leaf litter showed different trends than leaf litter inputs. The sine curve shifted to the right in SF,  
217 indicating that leaf input occurred just after the rainiest periods (peak in April; edf = 3.5; Fig. 5j)  
218 and abandoned AFS (minimum in November and maximum in February; edf = 5.6; Fig. 5k). No  
219 seasonal patterns were observed for leaf litter of managed AFS (edf = 1; Fig. 5f,i,l).

220 Total annual litter fall in the riparian zone of the abandoned AFS, managed AFS, and secondary  
221 forest was 1889, 1016, and 1176 g m<sup>-2</sup> yr<sup>-1</sup>, respectively. In the abandoned and managed AFS,  
222 56% of the terrestrial litter input (TI) was deposited on the forest floor and 44% directly entered  
223 the streams through vertical litter input (VI). In the secondary forest, the percentages of TI and  
224 VI were 63% and 37%, respectively. In the managed AFS, 61% of the total litter fall in the  
225 riparian zone entered the stream by lateral movement and 39% remained in the riparian zone. In  
226 the abandoned AFS, only 15% entered the stream and 85% remained in the riparian zone. The  
227 corresponding percentages in the secondary forest were 30 and 70%. The average annual total  
228 litter standing stock in the managed AFS was more than two times lower than in the abandoned  
229 AFS and more than three times lower than in the secondary forest (Fig. 6).

230

## 231 Discussion

232 Riparian zones with natural vegetation are important for the structural and functional integrity of  
233 streams (Gonçalves Junior et al., 2014, Rezende et al., 2017b). Our results on the contribution of

234 leaf litter in forests subject to different management practices are important information to assess  
235 the role of cocoa agroforestry in efforts to restore impacted forests in northeastern Brazil.  
236 Previous studies in the area have reported that the cocoa agroforestry system alters the  
237 biogeochemistry of C and N in streams and soils (Costa et al., 2017, 2018, Souza et al., 2017).  
238 However, these studies could not determine which forest attributes determined the observed  
239 changes in C and N cycling. Although differences between forests could be associated with  
240 different management regimes, it is necessary also to consider the potential influence of other  
241 factors that could not be evaluated in those study.

242 High litter production in the abandoned AFS may be due to the riparian vegetation structure  
243 (Gonçalves Junior et al., 2014; Rezende et al., 2017a) and successional stage during forest  
244 recovery (Sambuichi & Haridasan, 2007; Rolim et al., 2017). Factors such as abundant deposits  
245 of crop biomass (Beer et al., 1998), which are related to high carbon stocks in the soil (Gama-  
246 Rodrigues et al., 2010; Costa et al., 2018), and rapid nutrient cycling in these systems (Nair et al.,  
247 1999) are likely to play a role. The pattern of litter inputs in the abandoned AFS was more  
248 similar to that in the secondary forest than the managed AFS. Streams in abandoned AFS are  
249 usually lined by riparian vegetation (Ferreira et al., 2019) similar to that of streams in secondary  
250 forest, whereas in managed AFS, native shade trees are replaced by species with high  
251 commercial value (Cassano et al., 2009, Piasentin Saito & Sambuichi, 2014). Additional factors  
252 linked to higher litter production in abandoned AFS (Gama-Rodrigues et al., 2010) include  
253 greater stand age of the vegetation. Moreover, leaf surface area may be greater in the shaded  
254 stands where low solar radiation limits rates of photosynthesis (Beer et al., 1998). These factors  
255 tend to increase litter production, to which leaves contribute the largest fraction (Gonçalves  
256 Junior et al., 2014; Bambi et al., 2016; Tonin et al., 2017).

257 Higher litter production in the abandoned AFS is reflected in the observed spatial and seasonal  
258 patterns of litter inputs and standing stocks, which were also closer to those in the secondary  
259 forest than in the managed AFS. This indicates that abandoned AFS with little human  
260 intervention may provide favorable conditions for forest regeneration (Rolim et al., 2017) and  
261 could thus be valuable strategic sites for the conservation of riparian forest remnants in these  
262 agroforestry systems of Brazil (Faria et al., 2007; Cassano et al., 2009; Scroth et al., 2011;  
263 Sambuich et al., 2012). The presence of pioneer species in abandoned AFS could be a critical  
264 factor promoting this regeneration by facilitating ecological succession (Rolim & Chiarello 2004,  
265 Sambuichi & Haridasan 2007, Sambuichi et al. 2012).

266 Crop management, which involves hoeing and soil cleaning (Sambuichi et al., 2012; Mello &  
267 Gross, 2013), may be a critical factor accounting for the observed tendency of greater lateral  
268 litter inputs to streams in managed AFS. Possible mechanisms include facilitation of litter  
269 leaching and movement of litter along streams by runoff (Afonso, Henry & Rodella, 2000;  
270 Wantzen et al., 2008) as well as effects on the structure and composition of the tree vegetation  
271 (Deheuvels et al., 2014). Furthermore, some management practices introduce exotic species  
272 necessary for cultivation (Sambuichi, 2002; Piasentin, Saito & Sambuichi, 2014; Rolim et al.,  
273 2017) and involve thinning of the vegetation to obtain the desired shade levels for crop  
274 production (Johns, 1999).

275 The management practices in cocoa cultivation and phenology of the shade species may also  
276 have determined the greater contribution of reproductive plant parts in the managed AFS. This  
277 observation is related to the high proportion of exotic species (e.g. *Artocarpus heterophyllus*,  
278 *Spondias mombin* and, particularly in this study, *Clitoria fairchildiana*), which show a different  
279 phenology than native riparian forests (Sambuichi & Haridasan, 2007; Sambuichi et al., 2012).

280 Furthermore, variation in the size, shape, texture and anatomy of reproductive plant parts of  
281 different tree species in different forest types could account for the higher contribution of this  
282 litter fraction in managed AFS. This applies particularly to fruits of the legume *Clitoria*  
283 *fairchildiana*, the species contributing most to the reproductive plant parts in litter vertical inputs  
284 and standing stocks in this forest. The large dry and dehiscent fruits of the tree are 25 to 30 cm  
285 long and 2.6 to 2.9 cm wide (Silva & M<sup>o</sup>ro, 2008; Rezende et al., 2017). A potentially higher  
286 nutritional quality of such reproductive plant parts compared to leaves may favor rapid  
287 decomposition of the litter supplied to tropical streams. However, the fruits of *Clitoria*  
288 *fairchildiana* and other species in the managed AFS we investigated may not provide a high-  
289 quality nutritional resource (Rezende et al., 2017), and we do not currently have data to evaluate  
290 the consequences for litter decomposition.

291 Litter standing stocks in ecosystems are the net result of litter inputs and losses by movement and  
292 decomposition (Elosegi & Pozo, 2005; Tank et al., 2010). The high standing stocks we observed  
293 in streams of secondary forests could imply high inputs (França et al., 2009; Lisboa et al., 2015;  
294 Bambi et al., 2016) combined with slow decomposition and downstream transport (Gonçalves  
295 J<sup>u</sup>nior et al., 2014; Rezende et al., 2017a), and the high proportion of miscellaneous matter in the  
296 secondary forest stream could be due to the particularly slow decomposition of this organic matter  
297 fraction. Effective litter retention favors long residence times in streams (Bilby & Likens, 1980)  
298 and the generation of small organic particles released during decomposition (Gessner et al.,  
299 1999, Boyero et al., 2011) instead of coarse litter being transported downstream. This contrasts  
300 with the situation in the managed AFS where cocoa leaves are the predominant litter type, the  
301 high lignin and cellulose concentrations of which slow litter decomposition in the soil of cocoa  
302 AFS (Dawoe, Isaac & Quashie-Sam, 2010) and likely also in streams (Tank et al., 2010; Lemes

303 da Silva et al., 2017). In the managed AFS, in contrast, it may have been the high proportion of  
304 recalcitrant reproductive plant parts (see above) that favored high benthic standing stocks. This  
305 type of litter was rare in the secondary forest and abandoned AFS.  
306 Our finding that litter inputs and standing stocks in the abandoned AFS were more similar to  
307 those in the secondary forest than in the managed cocoa AFS suggests that abandoning  
308 management measures, such as litter removal and soil cleaning, could create favorable conditions  
309 for reestablishing natural litter dynamics in riparian zones and streams of former AFSs. The  
310 capacity of tree species richness to regenerate is high in those forests (Sambuichi & Haridasan,  
311 2007), if surrounding vegetation remains intact to provide a seed source for forest recovery  
312 (Rolim et al., 2017). It appears that the absence of management in the riparian zone of  
313 abandoned AFS sufficiently reduces pressure on species during regeneration (Rolim et al., 2017)  
314 for the phenology of species to become the main factor determining litter dynamics. Intensive  
315 management, in contrast, overrides the importance of phenology by altering the structure of  
316 riparian plant communities (DeLong & Brusven, 1994; Ferreira et al. 2019).

317

### 318 **Conclusion**

319 Although our study was restricted to one location for each of the three investigated forest types  
320 (SF, AC and MC), our findings are a starting point to evaluate differences in litter inputs and  
321 standing stocks between those forests. The observed similarity with litter inputs and standing  
322 stocks in the secondary forest suggests potential of the abandoned AFS to provide favorable  
323 conditions for restoring natural litter dynamics in streams and riparian zones. However, future  
324 investigations are needed to elucidate the nutritional quality of litter and its variation depending  
325 on the composition and structure of the riparian vegetation.

326

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331

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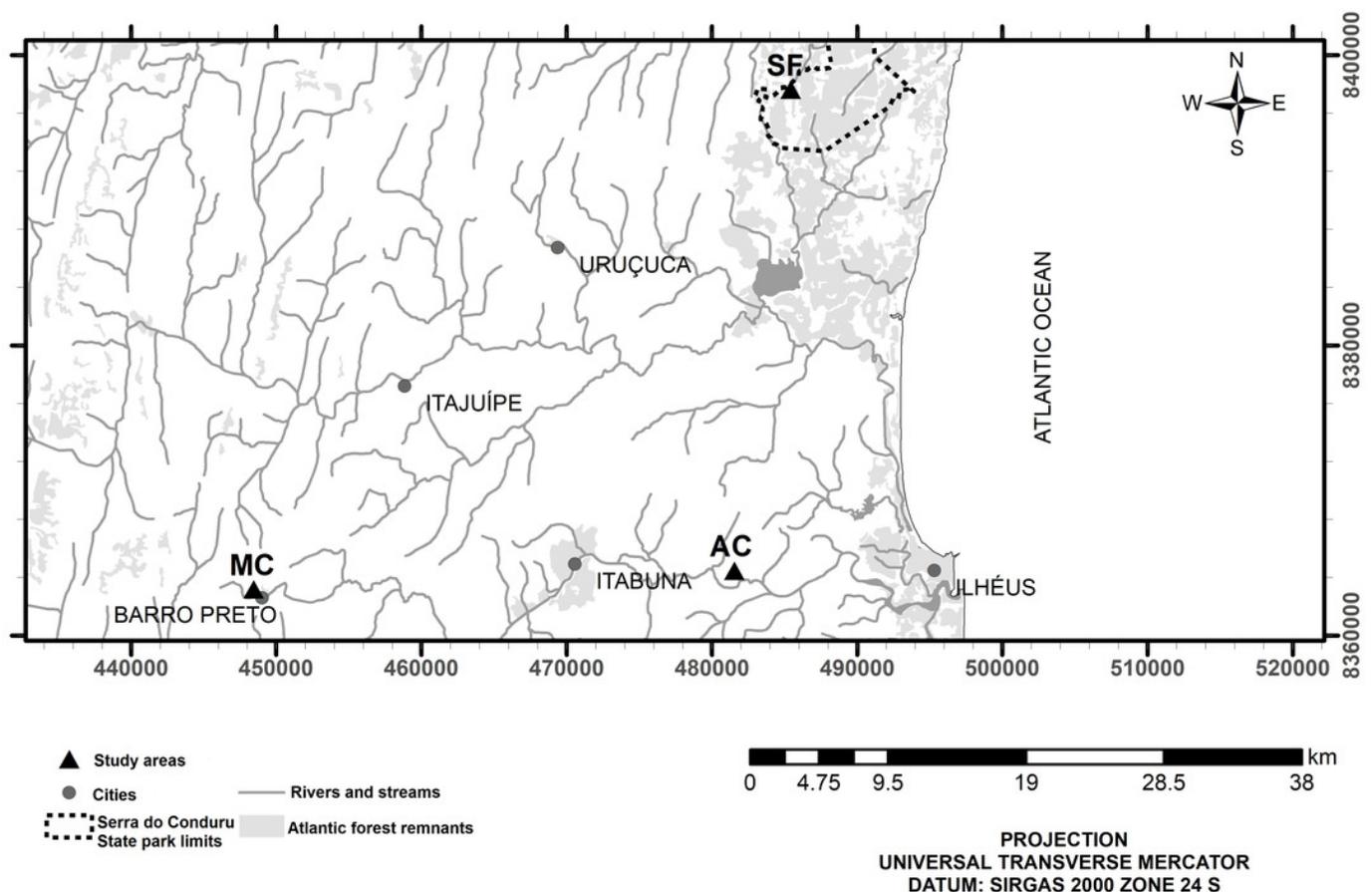
534

535

# Figure 1

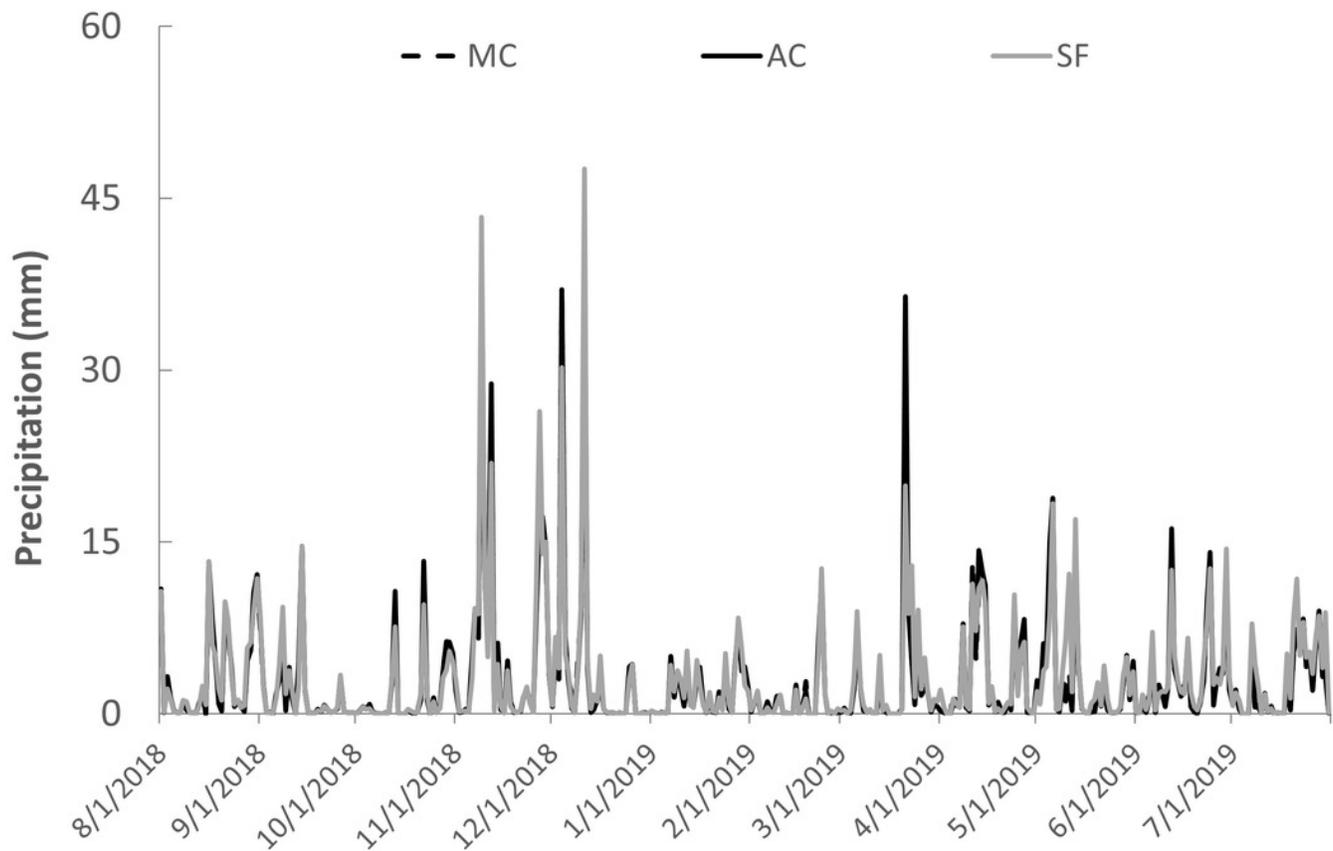
Location of study sites in secondary forest (SF), a managed AFS (MC) and an abandoned AFS (AC) in northeastern Brazil

Map database: Instituto Brasileiro de Geografia e Estatística (Brazilian territory, cities and hydrography, 2017); Ministério do Meio Ambiente (Serra do Conduru State Park limits, 2012), Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais (Atlantic Forest remnants, 2016).



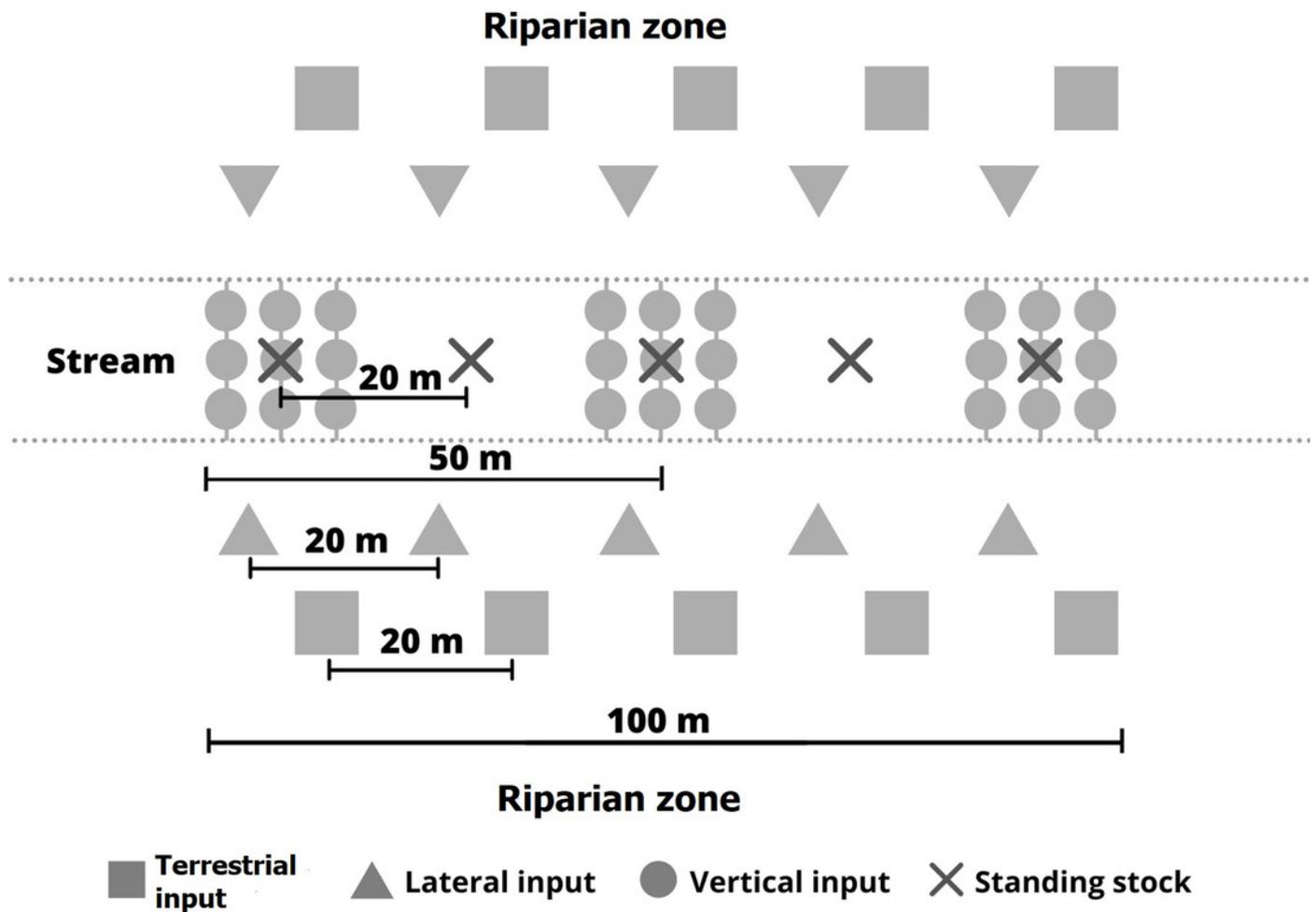
## Figure 2

Daily precipitation at the study sites in secondary forest (SF), a managed AFS (MC) and an abandoned AFS (AC) in northeastern Brazil



## Figure 3

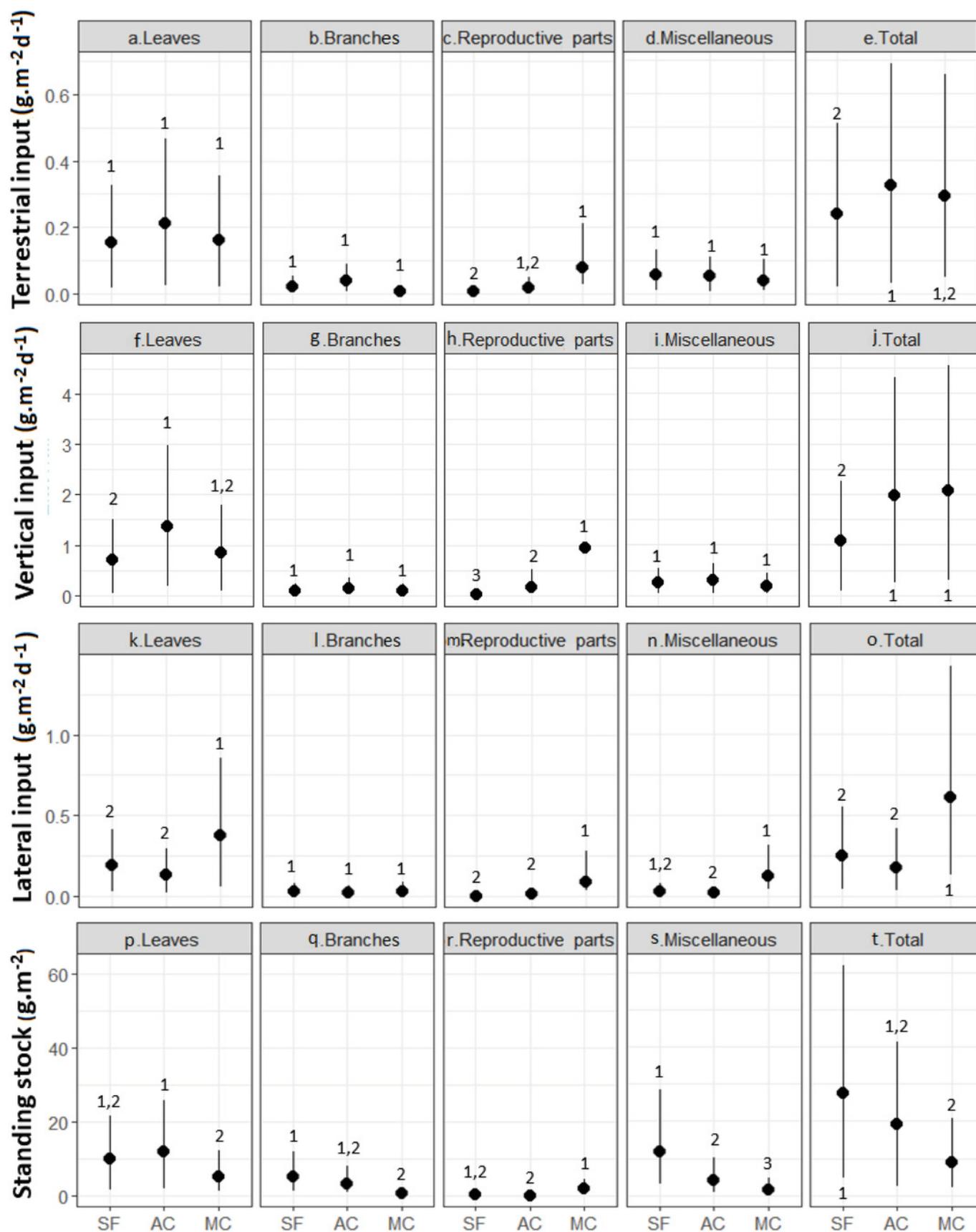
Sampling design to determine litter inputs and standing stocks in riparian zone and streams



## Figure 4

Inputs and standing stocks of various litter fractions in streams and riparian zones of secondary forest (SF), a managed AFS (MC) and an abandoned AFS (AC).

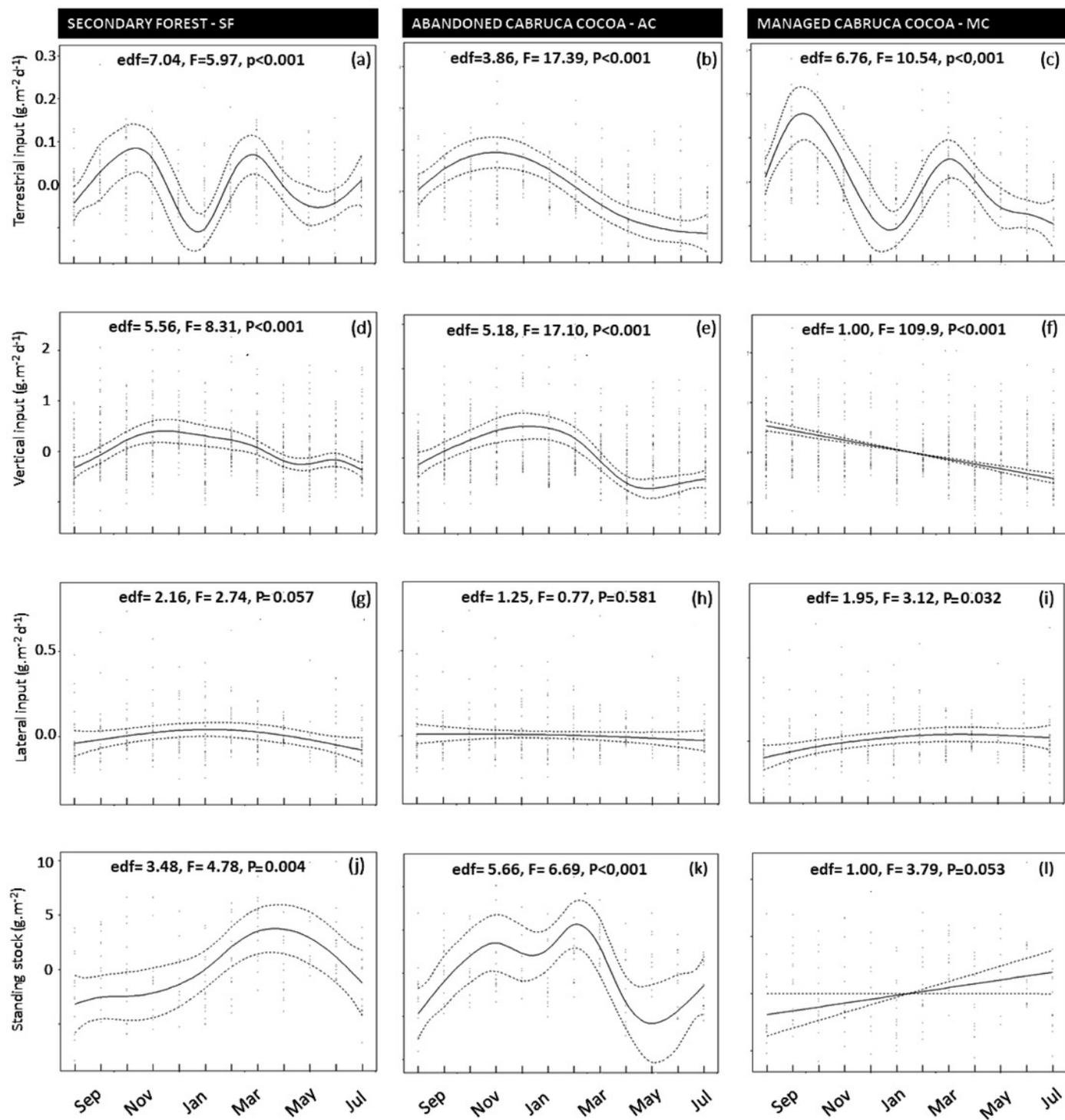
Black circles and vertical lines represent means and bootstrapped 95% confidence intervals. Different numbers indicate significant differences of means as judged based on non-overlapping confidence intervals.



## Figure 5

Temporal changes of litter inputs ( $\text{g dry mass m}^{-2} \text{d}^{-1}$ ) and standing stocks ( $\text{g dry mass m}^{-2}$ ) in secondary forest (SF), an abandoned AFS (AC) and a managed AFS (MC).

Also shown are F and P values as well as the effective degrees of freedom (edf) of GAMM analyses. Continuous lines are the GAMM smoothers and dotted lines indicate 95% confidence limits.

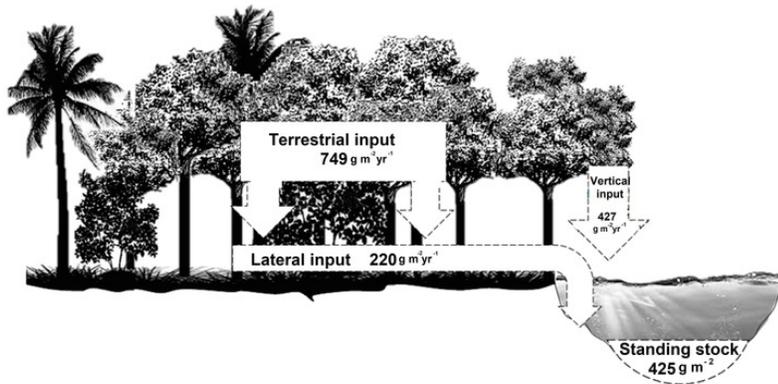


## Figure 6

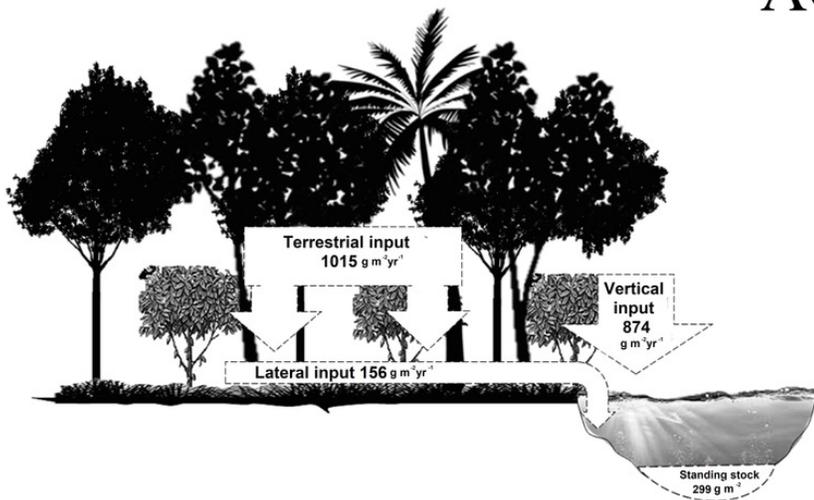
Summary of annual litter inputs and average standing stocks (g dry mass m<sup>-2</sup>) in streams and riparian zones

SF - secondary forest, AC- abandoned AFS and MC - managed AFS

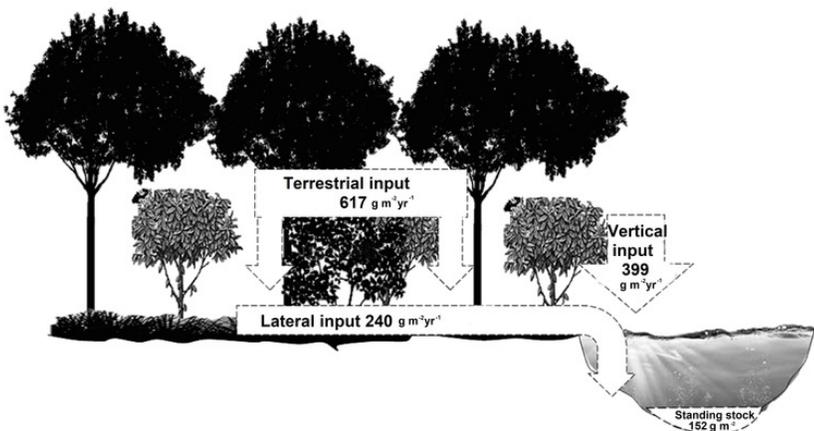
SF



AC



MC



**Table 1** (on next page)

Absolute monthly inputs and standing stocks ( $\text{g m}^{-2}$ ) as well as relative contributions (%) of various litter fractions to litter inputs and standings stocks in streams and riparian zones

Secondary Forest (SF), Managed AFS (MC) and Abandoned AFS (AC)

Litter fraction	Forest type	Terrestrial			Vertical input			Lateral input			Standing stock		
		Mean (g m <sup>-2</sup> )	Range (g m <sup>-2</sup> )	Contribution (%)	Mean (g m <sup>-2</sup> )	Range (g m <sup>-2</sup> )	Contribution (%)	Mean (g m <sup>-2</sup> )	Range (g m <sup>-2</sup> )	Contribution (%)	Mean (g m <sup>-2</sup> )	Range (g m <sup>-2</sup> )	Contribution (%)
Leaves	SF	48	0 – 76	65	27	0 – 122	67	18	0 – 164	74	153	6 – 483	36
	MC	50	0 – 193	56	30	0 – 194	41	28	0 – 441	65	91	0 – 422	60
	AC	64	4 – 322	67	56	0 – 287	69	12	0 – 5160	80	182	30 – 424	61
Branches	SF	6	0 – 92	8	3	0 – 201	8	3	0 – 83	13	81	0 – 431	19
	MC	2	0 – 48	3	3	0 – 137	4	2	0 – 103	5	10	0 – 95	7
	AC	12	0 – 75	12	6	0 – 86	7	1	0 – 99	7	48	0 – 386	16
Reproductive parts	SF	3	0 – 32	4	1	0-33	2	0	0 – 15	0	7	0 – 76	2
	MC	25	0 – 398	28	33	0 – 493	46	7	0 – 389	16	23	0 – 289	15
	AC	6	0 – 73	6	7	0 – 306	9	1	0 – 62	7	2	0 – 57	1
Miscellaneous litter	SF	17	0 – 137	23	9	0 – 108	23	3	0 – 63	13	185	0 – 1432	43
	MC	12	0 – 217	13	7	0 – 137	9	6	0 – 293	14	28	0 – 395	18
	AC	14	0 – 46	15	13	0 – 56	15	1	0 – 47	7	67	0 – 382	22
Total	SF	74	8 – 221	-	40	0 – 230	-	24	0 – 215	-	425	28 – 2050	-
	MC	89	0 – 511	-	69	0 – 638	-	43	0 – 816	-	152	0 – 559	-
	AC	96	4 – 339	-	82	0 – 521	-	15	0 – 303	-	299	78 – 726	-