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1 **Drivers of tree community assembly during tropical forest post-fire succession in**  
2 **anthropogenic savannas**

3

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19

20

21 **Abstract**

22 In the context of global change, tropical forests are increasingly affected by fires. Understanding the  
23 ecological processes driving forest recovery in fire-modified landscapes is a critical issue.

24 We analyzed spatial and temporal (8 years) changes in functional and phylogenetic composition of  
25 tree communities during forest post-fire recovery in anthropogenic savannas. We used null models  
26 to infer the main assembly processes driving forest succession along three 90-m transects running  
27 from an advancing savanna-forest edge to forest interior in New Caledonia. We also evaluated if  
28 successional changes differed between large and small trees, or depend on the demography of  
29 remnant savanna trees.

30 We found coordinated shifts from drought and fire resistance towards shade-tolerance strategies,  
31 involving leaf, stem, and architectural traits along transects. Our results indicate stronger  
32 environmental filtering and faster temporal changes in composition of young edge communities. In  
33 forest interior, our results suggest slower compositional changes, with an important role of light  
34 limitation in community assembly. These non-random patterns depended on both the decline of  
35 savanna trees and compositional changes among forest species. We also found contrasting  
36 community patterns depending on tree size, supporting a stronger influence of environmental  
37 filtering on small trees.

38 Our work emphasized the dominance of deterministic assembly processes driving tropical forest  
39 post-fire succession. Our study suggests that fire and drought drive environmental filtering during  
40 early succession at the forest edge, entailing constraints on multiple functional dimensions. As  
41 succession progresses, light-limitation became a stronger driver of community assembly, and  
42 community composition became more stable in time. Our study provides insights for a better  
43 understanding of the processes guiding tropical forest succession in the particular context of post-  
44 fire forest recovery.

45 Keywords: Tropical forest; Succession; Functional traits; Fire; Savanna; Assembly processes

## 46 **1. Introduction**

47 Tropical forest recovery maintains biodiversity and ecosystem services in human-modified  
48 landscapes (Arroyo-Rodríguez et al. 2017; Boukili and Chazdon 2017; Chai et al. 2016), and  
49 studying ecological successions allows to better understand, predict, and assist forest recovery  
50 (Buzzard et al., 2015, Cheesman et al., 2018). Specific successional pathways are often poorly  
51 known and vary with environmental context (Arroyo-Rodríguez et al., 2017; Boukili and Chazdon,  
52 2017; Lohbeck et al., 2013). Ongoing climate change and deforestation increase the influence of  
53 droughts and wildfires on tropical forests (Allen et al., 2010; Brando et al., 2014). Understanding  
54 how these factors affect the processes driving tropical tree assembly during forest recovery remains  
55 challenging (Boukili and Chazdon, 2017; Buzzard et al., 2015).

56 The assembly of tropical tree community depends on a range of ecological mechanisms spanning  
57 from deterministic, niche-based processes to neutral dynamics (Hubbell, 2001; Kraft et al., 2015).  
58 Niche theories predict that community assembly rely on species niche differences regarding biotic  
59 (i.e., species interactions) and abiotic (i.e., environmental filtering) constraints, while neutral theory  
60 assumes that community assembly depends only on stochastic immigration-drift dynamics (Adler et  
61 al., 2007). If environmental filtering drives community assembly, species establishment and  
62 survival should depend on how their ecological strategies match with local environmental  
63 conditions, and species occupying similar environments are expected to have similar, convergent  
64 strategies (Boukili and Chazdon, 2017, Kraft et al., 2015). Biotic interactions such as competition  
65 may entail either limiting similarity, i.e., divergence in species strategies (Abrams, 1983), or  
66 competitive dominance, i.e., the selection of species with similar competitive strategies and the  
67 exclusion of other species (Mayfield and Levine, 2010). Alternatively, without the influence of  
68 deterministic drivers, tree community assembly would rely on the sole influence of stochastic  
69 processes as predicted by the neutral theory, so that the composition of communities should be  
70 random with respect to species strategies (Swenson et al., 2012).

71 The successional pathway of tropical forest generally begins with the establishment of fast-growing,  
72 light-demanding pioneer species with acquisitive strategies (Chazdon, 2008; Lohbeck et al., 2013;  
73 Poorter et al., 2008; Swenson et al., 2012). Nonetheless, the influence of strong abiotic constraints  
74 (e.g., dryer conditions) at the beginning of the succession can entail environmental filtering,  
75 favoring species with conservative and resistance abilities (Buzzard et al., 2015; Fang et al., 2019;  
76 Letcher et al., 2012; Lohbeck et al., 2013). As succession progresses, the number and size of  
77 individuals increase and canopy closes, which causes an increase in the influence of the light  
78 limitation on species recruitment (Buzzard et al., 2015; Chazdon, 2008; Pacala et al. 1996). As more  
79 and more species establish during succession, biotic interactions are expected to play an increasing  
80 role in community assembly, entailing either limiting similarity (Letcher et al., 2012; Lohbeck et al.  
81 2014) or competitive dominance (Buzzard et al., 2015). If species strategies are sufficiently  
82 conserved across phylogenies (i.e., phylogenetically related species tend to have more similar  
83 strategies than less related species), niche-based assembly processes should likewise entail patterns  
84 of convergence or divergence in phylogenetic composition of communities (Cavender-Bares et al.  
85 2009; Mayfield and Levine, 2010, Swenson et al., 2012, 2013; Webb et al., 2002). Hence,  
86 investigating spatial and temporal changes in community phylogenetic structure can provide  
87 additional information about deterministic processes driving community assembly (Mouquet et al.  
88 2012, Swenson et al., 2012, 2013). Nonetheless, environmental filtering and competition can act  
89 together in shaping community composition, which can blur their respective signatures (Bernard-  
90 Verdier et al., 2012; Götzenberger et al., 2016). Processes driving forest succession can also act  
91 differently depending on tree size. Notably, some studies suggested that small trees may undergo  
92 stronger environmental filtering than older and larger canopy trees (Baldeck et al. 2013; Fang et al.,  
93 2019; Lasky et al., 2015). In addition, rapid shifts in constraining factors during forest succession  
94 should entail rapid changes in community composition, while compositional changes should be  
95 slower in late-successionnal communities where the environment is relatively constant (Swenson et  
96 al., 2012).

97 Forest-savanna landscapes are characterized by highly contrasting environments with sharp spatial  
98 transitions (Charles-Dominique et al., 2018; Gignoux et al., 2016; Ibanez et al., 2013a). In  
99 anthropogenic savannas, frequent anthropogenic fires maintains the coexistence of a flammable  
100 grass layer with an open-canopy tree layer (Hoffmann et al., 2009; Staver et al., 2011). In such  
101 environments, the establishment and survival of forest trees is strongly limited by fire (Cardoso et  
102 al., 2016, Hoffmann et al., 2009, 2012a, 2012b), while light is generally not a limiting factor  
103 (Charles-Dominique et al., 2018; Geiger et al., 2011). However, prolonged fire-free periods (i.e.,  
104 10-15 years) allow forest saplings to establish in savanna (Geiger et al., 2011; Hoffmann et al.,  
105 2012a). The influence of drought, which is amplified by low tree cover, can also limit the  
106 establishment of forest species in savanna (Hoffmann et al., 2012b; Ibanez et al., 2013a; Rossato et  
107 al., 2013). In addition, soil nutrient availability is generally lower in savannas than in forest areas  
108 (Silva et al., 2013). On the other hand, in forest interior, closed canopy provides wetter conditions  
109 that prevent fire progression and light availability becomes more limiting for species recruitment  
110 (Hoffmann et al., 2012b; Ibanez et al., 2013a). The boundary between these alternative ecosystem  
111 states is generally constituted by a distinct forest edge (Geiger et al., 2011, Ibanez et al., 2013a).  
112 Such environmental contrasts entail striking differences in strategies between savanna and forest  
113 species (Charles-Dominique et al., 2018; Hoffmann et al., 2012a; Maracahipes et al., 2018; Ratnam  
114 et al., 2011). Notably, the recruitment of light-demanding savanna species is limited by shading  
115 under a closed canopy, which can drive a progressive decline of remnant populations of savanna  
116 trees in regenerating forests (Charles-Dominique et al., 2018; Geiger et al., 2011). However, few  
117 studies have explicitly addressed how the environmental context associated with anthropogenic  
118 savannas influences the pathway of tropical forest succession according to species strategies  
119 (Cardoso et al., 2021).

120 Ecological strategies can be characterized based on species functional traits (Violle et al., 2007).  
121 Bark has a major functional role in protecting stem against external damage from fire, as well as  
122 various factors as drought and herbivory (Pausas, 2015; Rosell, 2016). Notably, thicker bark is

123 associated with higher survival rate in fire-prone areas (Charles-Dominique et al., 2017; Hoffmann  
124 et al., 2012a; Silva and Batalha, 2010). The leaf economic spectrum is a key functional dimension  
125 opposing acquisitive, fast-growing strategies based on low-cost, thin leaves with high  
126 photosynthetic rates, to conservative strategies with thick and long-lived leaves, more adapted to  
127 environments with low water and nutrient availability (Baraloto et al., 2010; Moles, 2018; Wright et  
128 al., 2004). In fire-prone landscapes, thicker and denser leaves also reduce leaf flammability (Pausas  
129 et al. 2017). Leaf area determines species transpiration surface and is negatively related with  
130 drought resistance (Wright et al., 2017). Furthermore, higher leaf area increases species capacity to  
131 intercept light, conferring greater competitive ability in light-limiting conditions (Díaz et al., 2016;  
132 Moles, 2018; Pierce et al., 2013). Another key functional trait of trees is wood density. Light wood  
133 is associated with high hydraulic efficiency, fast growth, but high mortality rate, while dense wood  
134 is associated with high drought resistance and mechanical support, slow growth, and low mortality  
135 rate (Chave et al., 2009). Finally, plant architecture determines light capture strategy, through  
136 horizontal and/or vertical space exploration, and should be related to competitive ability and shade  
137 tolerance (Ford, 2014; Küppers, 1989; Poorter et al., 2006). Specifically, vertical growth allows  
138 species to rapidly reach the canopy and have greater access to light, while lateral growth optimizes  
139 light capture under low light availability by both avoiding self-shading and increasing shading for  
140 adjacent competitors (Charles-Dominique et al., 2018; Gignoux et al., 2016; Millet et al., 1999). In  
141 a savanna context, trees have more space and light is less limiting, so that savanna species are  
142 generally smaller and invest less in vertical exploration than forest species (Charles-Dominique et  
143 al., 2018; Gignoux et al., 2016). In savannas, investing in vertical growth allows trees to quickly  
144 produce leaves and buds higher than flame height, and thus escape from fire injuries (Gignoux et  
145 al., 2016). Yet, although the influence of species architecture on their ability to compete has been  
146 suggested since three decades (Givnish, 1988; Küppers, 1989), little is known about its role  
147 regarding community-level assembly processes (Charles-Dominique et al., 2018; Ford, 2014;  
148 Subedi et al., 2019; Verbeeck et al., 2019).

149 In this study, we investigated the patterns of spatial (i.e., edge to interior) and temporal (i.e., 8 years  
150 interval) variations in the functional and phylogenetic composition of tree communities along a  
151 savanna-to-forest transition in New Caledonia. We focused on key functional traits representing  
152 drought and fire resistance, resource-use and light capture strategies to characterize the successional  
153 pathways leading to forest expansion in savanna. In light of these patterns, we inferred the  
154 processes that are likely to drive forest recovery and succession in anthropogenic savannas. Our  
155 general hypothesis was that the prevailing drivers of community assembly shift from environmental  
156 filtering related to fire and drought at the forest edge, where post-fire succession starts, to increasing  
157 light limitation in forest interior communities. Using a null model approach, we addressed several  
158 expectations in line with this hypothesis. We expected spatial trait patterns to reflect a shift from  
159 fire- and drought-resistance, as well as light-demanding strategies in young edge communities, to  
160 shade-tolerance strategies in forest interior. If constraints generated by environmental filtering are  
161 relaxed during succession, we should observe an increase in functional and phylogenetic diversity  
162 from the edge to forest interior. Then, if succession progressed during the studied time interval, we  
163 expected temporal change in community mean trait values to reflect a successional pathway similar  
164 to the one revealed by spatial patterns. Finally, we expected temporal change in taxonomic,  
165 functional and phylogenetic composition to be faster in younger edge communities than in forest  
166 interior, where recruitment limitation should be stronger and environmental conditions should be  
167 more stable. Because different tree size classes may undergo different constraints during succession,  
168 we evaluated if the observed spatial and temporal changes in community composition differed  
169 between small and large trees. As areas of recent forest recolonization included remnant savanna  
170 trees (*Melaleuca quinquenervia*, Myrtaceae), we also assessed whether the signature of changing  
171 assembly processes relied on the traits and demography of savanna species or if they reflect  
172 congruent compositional shifts among forest species.

173

## 174 **2. Material and Methods**



175 **2.1. Study site and data collection**

176 The study site is located at 450m a.s.l. on the western side of the Aoupinié mountain reserve (21° 11  
177 0 S, 165° 15 0 E), in the central mountain chain of New Caledonia's main Island (southwest pacific,  
178 20–23° S, 164–167° E, 0-1628m a.s.l.). The site receives a mean annual rainfall of 2500 mm and  
179 mean annual temperature is approximately 20C° (Météo France Nouvelle-Calédonie, 2012).  
180 Seasonality is characterized by a short dry season (3-4 months) with increased fire frequency, which  
181 can be accentuated by the *El Nino* Southern Oscillation (ENSO) phenomenon (Curt et al., 2015).  
182 The vegetation of the studied area consists in a mosaic of forest and savanna maintained by frequent  
183 anthropogenic fires (Ibanez et al., 2013b, 2013c), and is representative of low to middle elevation  
184 vegetation found on volcano-sedimentary soils in New Caledonia (Jaffré et al., 1998).

185 The tree layer of New Caledonian savanna is almost exclusively dominated by the savanna-  
186 specialist *Melaleuca quinquenervia* (Myrtaceae, native of New Caledonia and the east coast of  
187 Australia and Papua New Guinea), while the flammable grass layer is dominated by a mixture of  
188 exotic species (Ibanez et al., 2013c; Jaffré et al., 1994). We revisited and surveyed three transects  
189 (120-m long, 20-m wide, and spaced 50m apart) set up by Ibanez et al. (2013b) in 2010. The  
190 transects were disposed perpendicularly to the savanna-forest edge, and set 30m from the edge in  
191 the savanna to 90m from the edge in the forest (see Ibanez et al., 2013b for detailed protocol). The  
192 forest area extending within the first 40m from the edge results from recent forest recovery on  
193 savanna. This is supported both by the analysis of a time series of aerial photographs showing forest  
194 margin expansion on savanna (Ibanez et al., 2013c), and by the presence of remnant *Melaleuca*  
195 *quinquenervia* in the forest canopy as a legacy of the former savanna (Ibanez, et al., 2013b).

196 In 2010, along each transects, all trees with a diameter at breast height (DBH)  $\geq$  5cm were  
197 identified at the species level, tagged, and mapped (see Ibanez et al., 2013b), resulting in a total of  
198 1435 individuals recorded in the forest part of the three transects (478 on average). In 2018, each  
199 transect was re-surveyed following the exact same protocol. During this second census, 118 trees  
200 that were previously recorded in 2010 were dead, and 126 new trees (DBH  $\geq$  5cm) were recorded in

201 the transects. Between 2010 and 2018, a total of 112 tree species were identified (palms, ferns and  
202 lianas were not considered in the analyses). It is important to note that we observed fire marks  
203 indicating savanna fire occurrence near the forest edge between 2010 and 2018. In order to analyze  
204 variation of community composition along transects, we subdivided the forest part of each transect  
205 (i.e., from the edge to 90m towards the forest core) into nine 200m<sup>2</sup> plots (10m × 20m), resulting in  
206 a total of 27 forest subsamples (Fig. 1), with an average an standard deviation of 21±5 species and  
207 53±10 individuals per subsamples (data from 2010). This subdivision in 27 subsamples provided a  
208 good compromise between sample size and spatial resolution. These 27 subsamples distributed  
209 along transects were considered as distinct tree communities in further analyses. We expected  
210 spatial and temporal compositional changes within and among these communities to reflect the  
211 influence of processes driving forest succession.

212

## 213 ***2.2. Groups of edge and forest interior communities***

214 In order to test if different local and temporal diversity patterns occurred in communities located  
215 near the edge and in communities of forest interior, we performed a preliminary analysis to  
216 differentiate groups of communities (S1). We computed a floristic dissimilarity matrix using the  
217 Bray-Curtis index based on species abundances in communities (see Ibanez et al., 2013c). As the  
218 successional status was known to vary across communities depending on the distance from the edge  
219 (Ibanez et al., 2013c), we then applied a hierarchical clustering on the dissimilarity matrix with the  
220 Ward method to discriminate groups between younger edge communities and forest interior  
221 communities (S1). We tested the significance of groups by performing a similarity profile test  
222 (SIMPROF, Clarke et al. 2008) with 1000 permutations (abundances of each species in  
223 communities are permuted independently and similarity profiles are recalculated, R package  
224 *clustsig*, Whitaker and Christman, 2014). As floristic composition varies among transects (mean  
225 Bray-Curtis dissimilarity is 0.48, see Ibanez et al., 2013c for more details), this method was applied  
226 separately within each transect. This yielded identical clustering patterns among transect with

227 respect to distance from edge: the four communities located between 0-40m from edge were  
228 classified as edge communities and the five communities located between 40-90m from edge were  
229 classified as forest interior communities (S1). Note that, in transect 2, two sub-groups of  
230 communities were significantly different within forest interior communities, but were not  
231 considered as different in further analyses.

232

### 233 ***2.3. Spatial and temporal turnover in species composition***

234 To contextualize our functional and phylogenetic analyses, we used Bray-Curtis dissimilarities to  
235 assessed the spatial and temporal changes in species presence/absence and abundance. We  
236 computed Bray-Curtis dissimilarities (function *vegdist* from *vegan* R package, Oksanen et al. 2020)  
237 between pairs of communities located in each transect to evaluate the spatial taxonomic turnover. In  
238 order to estimate the temporal turnover in taxonomic composition, we also computed Bray-Curtis  
239 dissimilarities by comparing the compositions of each community between 2010 and 2018. To  
240 evaluate if the changes in taxonomic composition relied on species turnover or only on changes in  
241 species abundances, spatial and temporal dissimilarities were computed either by considering  
242 species abundance (i.e., abundance-based dissimilarities) or presence-absence (i.e., species-based  
243 dissimilarities). *Melaleuca quinquenervia* was excluded from this analysis in order to focus only on  
244 the turnover occurring among forest species. We then used linear models to test the relationships  
245 between spatial Bray-Curtis dissimilarity and the log-transformed distance between pairs of  
246 communities of each transect, and to test the relationships between temporal Bray-Curtis  
247 dissimilarity within communities and log-transformed distance from forest edge. We also used  
248 Wilcoxon signed rank tests to evaluate if temporal dissimilarity significantly differed between edge  
249 communities (i.e., communities located from the edge to 40m inside the forest) and forest interior  
250 communities (i.e., communities located further than 40m from the edge).

251

## 252 2.4. *Species traits*

253 We measured six functional traits involved in drought resistance, fire resistance, light capture, and  
254 resource-use strategies. Detailed functions associated with each traits are listed in Table 1. Traits  
255 were collected and measured during the 2018 survey, following the standardized protocols  
256 recommended by Pérez-Harguindeguy et al. (2013). We aggregated trait values at the species level  
257 as our study focused on species successional turnover.

258 We measured three leaf traits on five leaves per individual and five individuals per species. We  
259 collected healthy and sun-exposed leaves (or leaves most exposed to direct sunlight for understory  
260 species). For each species, leaves were collected from adult trees located at different distance from  
261 the edge, in order to account as much as possible for potential intraspecific variation. For compound  
262 leaves, we considered a leaflet as the laminar unit. Petioles and petiolules were removed from  
263 leaves before measurement. We measured Leaf Area (LA, the area of a leaf in  $\text{cm}^2$ ), Specific Leaf  
264 Area (SLA, the leaf area per dry mass in  $\text{cm}^2 \times \text{g}^{-1}$ ), and Leaf Dry-Matter Content (LDMC the leaf  
265 dry mass per fresh mass in  $\text{mg} \times \text{g}^{-1}$ ). LA values were log-transformed to correct for non-normality  
266 prior to analysis. We also collected two stem traits at breast height (i.e., 1.3 m above ground): Wood  
267 Density (WD) by collecting one wood sample (5.15mm diameter core) per individual on five  
268 individuals per species, and relative Bark Thickness (i.e., relative to stem radius, BT) by  
269 systematically measuring bark thickness at two opposite points on all individuals. Trait data were  
270 partially completed with data from the NC-PIPPN database (for 44 species for leaf traits, i.e., 50%  
271 of the dataset, and for 66 species for WD, i.e., 75% of the dataset) in which traits were collected in  
272 the same region and following the same standardized protocols (Blanchard et al., 2019, 2020;  
273 Ibanez et al., 2017). Branch orientation was determined for each species in the field (following  
274 methods described by Barthélémy and Caraglio, 2007). Species with horizontal branch growth and  
275 bilateral symmetry were denoted as “plagiotropic”, and species with vertical branch growth and  
276 radial symmetry were denoted as “orthotropic” (Barthelemy and Caraglio, 2007). For the few

277 species for which the orientation of branches vary through ontogeny, the modality of adult trees was  
278 considered.

279 Complete trait data were finally available for 88 species representing 79% of all identified tree  
280 species ( $n = 112$ ), and 95% of all recorded individuals ( $n = 1561$ ), including trees characterized as  
281 dead or recruits during the 2018 survey (see S2). At the community level, trait data were complete  
282 for a least 79 % (92% on average) of the species and 83% (94% on average) of the individuals. We  
283 used this species subset in further analyses.

284

## 285 **2.5. Community mean trait values**

286 For each of the 27 communities and each trait, we computed the Community Weighted Mean  
287 (CWM), i.e., the mean trait value of communities weighted by species abundances, at  $t0$  (2010, see  
288 S3) and  $t8$  (2018). CWM is a widely used trait-based statistic aiming to track changes in community  
289 mean trait values, which is expected to reflect trait-environment relationships (Ackerly and  
290 Cornwell, 2007; Bernard-Verdier et al., 2012). To analyze temporal variation of community mean  
291 trait values, we computed  $\Delta\text{CWM}$ , as the difference between CWM at  $t8$  and CWM at  $t0$ . In order  
292 to assess if spatial and temporal variation in mean trait values depended only on the distribution and  
293 dynamics of the savanna species *M. quinquenervia*, CWM and  $\Delta\text{CWM}$  were computed either with  
294 and without this species in the dataset (see S3).

295

## 296 **2.6. Functional and phylogenetic dendrograms**

297 To quantify functional dissimilarity between species, we first computed a Gower's distance matrix  
298 of species trait values (traits were standardized by subtracting mean value and dividing by the mean  
299 absolute deviation), as recommended by Mouchet et al. (2008) for a mixture of quantitative and  
300 qualitative traits. Then, we built a dendrogram based on functional dissimilarities by applying a

301 hierarchical clustering with the group average method on the distance matrix (see S4a), which  
302 preserves most of the initial distances from the multidimensional trait space (Mouchet et al. 2008).

303 To quantify community phylogenetic diversity, we built a phylogenetic tree at the species level. We  
304 used the molecular angiosperm family dated tree of Magallón et al. (2015) to assess all angiosperm  
305 familial relationships and divergence times. We pruned the phylogenetic tree to retain only families  
306 that occurred in our dataset. We then added tips corresponding to all genus present in our dataset. As  
307 nodes located between family and genus were undated, their ages were evenly interpolated between  
308 family nodes and tips. Finally, we built a species tree by adding species to their corresponding  
309 genus (see S4b). Polytomies were used within genus including several species (37.5% species were  
310 in polytomies). Species divergence times were set as half the age of the corresponding genus with a  
311 maximum of 37 Myrs (i.e. corresponding to the estimated date of final emergence of New  
312 Caledonia) based on the phylogenetic hypothesis that New Caledonia's flora mostly results from  
313 post-emergence colonization events (Schlessman et al., 2014).

314

## 315 **2.7. Phylogenetic signal**

316 To assess if functional relatedness was related to phylogenetic distance between species, we  
317 evaluated the phylogenetic signal in species traits (Mayfield and Levine, 2010; Münkemüller et al.,  
318 2012). If measured traits show low phylogenetic signal, community phylogenetic patterns may  
319 reflect assembly processes acting on unmeasured traits (Swenson et al. 2012). We therefore  
320 computed Pagel's  $\lambda$  (Pagel 1999), which is robust to polytomies (Molina-Venegas and Rodríguez,  
321 2017), using the phytools R package (Revell, 2012). For Pagel's  $\lambda$ , a value of one indicates a  
322 distribution of trait corresponding to a Brownian motion of evolution. Values higher than one  
323 indicate stronger phylogenetic signal than expected under a Brownian motion, while values close to  
324 zero suggest phylogenetic independence (Münkemüller et al., 2012; Pagel, 1999). We tested  
325 phylogenetic signal in plagiotropy using the *D*-statistic of Fritz and Purvis (2010) for binary traits.

326 For the  $D$ -statistic, a value close to or higher than one indicates weak phylogenetic signal, while a  
327 value close to or lower than zero indicates strong phylogenetic signal.

328

## 329 **2.8. Functional and phylogenetic diversity**

330 In order to evaluate changes in functional and phylogenetic diversity along transects, we computed  
331 functional and phylogenetic abundance-weighted mean pairwise distance between species (FMPD  
332 and PMPD, respectively) within each community. FMPD and PMPD represent the mean functional  
333 and phylogenetic distances between species occurring in a given community, as measured using  
334 functional and phylogenetic dendrograms, weighted by species abundances (Webb et al., 2002).

335

## 336 **2.9. Functional and phylogenetic temporal changes**

337 To evaluate the rate of temporal changes in community composition, we used the abundance-  
338 weighted mean pairwise functional and phylogenetic dissimilarity indexes ( $FD_{pw}$  and  $PD_{pw}$ ,  
339 respectively) proposed by Swenson et al. (2012):

$$D_{pw} = f_A \sum_{i=1}^{S_A} f_i \overline{\delta_{ib}} + f_B \sum_{j=1}^{S_B} f_j \overline{\delta_{ja}}$$

340 where  $S_A$  and  $S_B$  are the number of species in the community at time A and B,  $f_i$  and  $f_j$  are the  
341 relative abundances of species  $i$  in the community at time A and of species  $j$  in the community at  
342 time B, respectively.  $\overline{\delta_{ib}}$  is the mean pairwise functional or phylogenetic distance between species  $i$   
343 in the community at time A and all species in the community at time B, and  $\overline{\delta_{ja}}$  is the mean pairwise  
344 functional or phylogenetic distance between species  $j$  in the community at time B and all species in  
345 the community at time A.  $f_A$  and  $f_B$  are the relative abundances of individuals in the community at  
346 time A and B, respectively.  $f_A$  is therefore defined as the number of individuals in the community at

347 time A divided by the sum of the number of individuals in community at time A and the number of  
348 individuals in community at time B (Swenson et al., 2012).

349

### 350 **2.10. Null model testing**

351 We devised two null models to evaluate if spatial and temporal variation in community composition  
352 diverged from defined null hypotheses of random community assembly (Fig. 2, Götzenberger et al.,  
353 2012; Bernard-Verdier et al., 2012). Each null model consisted in the permutation of species  
354 attributes (i.e., functional traits and phylogenetic position) and were used to obtain null distributions  
355 of community statistics describing the functional and phylogenetic composition of communities  
356 (CWM, FMPD, PMPD) or temporal changes in this composition ( $\Delta$ CWM,  $FD_{pw}$  and  $PD_{pw}$ ). This  
357 procedure allows testing if the observed spatial and temporal changes in community composition  
358 are non-random with respect to species attributes (Swenson et al., 2012). Non-randomness should  
359 indicate that niche-based processes are dominant in driving community assembly, while no  
360 deviation from randomness would suggest that community assembly is predominantly driven by  
361 stochastic processes (Swenson et al., 2012). Both functional and phylogenetic information are used  
362 at the species level, implying that any change in functional or phylogenetic composition reflect a  
363 change in species composition. For each null model, we performed 9999 randomizations and  
364 species attributes were always permuted jointly, that is, keeping the same sets of trait value and  
365 phylogenetic position.

366 The first null model (NM1) was used to test if spatial changes in community composition observed  
367 in 2010 along transects occurred randomly with respect to species attributes. In NM1, the attributes  
368 (traits and phylogenetic position) of species occurring in 2010 were jointly permuted between  
369 species at the transect level (Fig. 2). Such randomization has been recommended to test for the  
370 influence of environmental filtering and limiting similarity along environmental gradients  
371 (Götzenberger et al., 2012). NM1 was used to obtain null distributions of CWM, FMPD and PMPD.



372 Non-random spatial variations in CWM along the transects were expected to reflect spatial changes  
373 in environmental filtering and/or biotic interactions constraining species traits distribution in  
374 communities. We expected that CWM would shift from trait values associated with fire and drought  
375 resistance at the edge, to trait values related to shade tolerance in forest interior (Fig. 2). Lower  
376 FMPD or PMPD than expected (i.e., functional or phylogenetic clustering) were interpreted as a  
377 convergence of species ecological strategies, which should occur under the dominant influence of  
378 environmental filtering. Inversely, higher FMPD or PMPD than null model expectation should  
379 indicate divergence in species strategies, as expected under the dominant influence of limiting  
380 similarity. If environmental constraints are relaxed during the succession FMPD and PMPD should  
381 increase from younger edge communities to forest interior.

382 The second null model (NM2) was used to test if temporal changes in species composition within  
383 communities between 2010 and 2018 occurred randomly with respect to species attributes. In NM2,  
384 species attributes (traits and phylogenetic position) were jointly permuted among the list of species  
385 occurring within each community in either 2010 or 2018 (Fig. 2). This broke the link between  
386 species attributes and temporal changes in abundances within communities while maintaining  
387 species identity and attributes between the two censuses at each permutation. We used NM2 to  
388 produce null distributions of  $\Delta\text{CWM}$ ,  $\text{FD}_{pw}$  and  $\text{PD}_{pw}$ . We interpreted non-random variation in  
389  $\Delta\text{CWM}$  as temporal changes in the influence of environmental filtering and biotic interactions on  
390 species traits within communities. If succession progressed during the studied time interval,  $\Delta\text{CWM}$   
391 should shift towards less fire- and drought-resistant trait values in edge communities (Fig. 2). We  
392 interpreted higher or lower  $\text{FD}_{pw}$  and  $\text{PD}_{pw}$  than expected by chance as respectively faster or slower  
393 functional and phylogenetic temporal changes in communities (i.e., replacement of older trees by  
394 functionally and phylogenetically more dissimilar, or more similar species, Swenson et al., 2012).  
395 Thus, we expected  $\text{FD}_{pw}$  and  $\text{PD}_{pw}$  to be higher in communities near the edge where changing  
396 environmental constraints should entail rapid changes in species strategies (Fig. 2).

397 An effect size was used to evaluate the divergence of the observed values of each community  
398 statistics from their null distributions :

399

$$ES = \left( \left( \frac{\text{number}(I_{null} < I_{obs}) + \frac{\text{number}(I_{null} = I_{obs})}{2}}{10000} \right) - 0.5 \right) \times 2$$

400 where  $I_{obs}$  was a given observed community statistics and  $I_{null}$  was its null distribution computed  
401 from 9999 values under a given null model (see Bernard-Verdier et al., 2012). ES is the probability  
402 that the observed value is lower than expected minus 0.5 and multiplied by 2, and thus varies  
403 between -1 and 1. Therefore, negative or positive values of ES respectively indicate lower or higher  
404 observed values of community statistics than expected under null models. Since non-random  
405 distribution of species abundances across phylogeny can bias such null model testing for  
406 phylogenetic statistics (Hardy, 2008), we have preliminary tested for phylogenetic signal in species  
407 abundances (using the same method than for traits), which was not significant (Pagel's  $\lambda = 0.31$ , p-  
408 value = 0.69).

409

## 410 ***2.11. Statistical analyses***

411 In order to assess if significant spatial and temporal changes in community composition occurred  
412 along succession, we tested the relationships between ES values of each community statistics and  
413 the log-transformed distance from forest edge (Fig. 2) using linear models (residuals of all models  
414 were normally distributed and homoscedastic). In addition, we used one-sample Wilcoxon signed  
415 rank tests to evaluate if ES values of all edge communities (i.e., communities located from the edge  
416 to 40m inside the forest) or all forest interior communities (i.e., communities located at more than  
417 40m from the edge) significantly diverged from zero (i.e., diverged from random species  
418 composition with respect to species attributes as expected in either NM1 or NM2). This approach

419 was conducted separately for all trees, small trees ( $5\text{cm} \leq \text{DBH} < 10\text{cm}$ , 45.7% of individuals) and  
420 large trees ( $\text{DBH} \geq 10\text{cm}$ , 54.3% of individuals) in order to evaluate if spatial and temporal changes  
421 in community composition differ among tree size classes. Note that only 15 species, representing  
422 6% of all individuals, were exclusively inventoried among small trees (see S2). To assess if  
423 variation in ES resulted solely from the presence and demography of remnant savanna trees (*M.*  
424 *quinquenervia*) in forest communities or reflect significant compositional shifts among forest  
425 species, we applied the procedure with or without *M. quinquenervia* in the dataset.

426

### 427 **3. Results**

#### 428 ***3.1. Species traits and phylogenetic signal***

429 We found substantial variation among species for all measured traits (see S2 and S5). *M.*  
430 *Quinquenervia*, the savanna-specialist species, had lower LA, lower SLA, and higher BT than most  
431 forest species (i.e.,  $\text{LA} < 92\%$ ,  $\text{SLA} < 98\%$ , and  $\text{BT} > 98\%$  of forest species, see S2 and S5). Two  
432 thirds of forest species as well as *M. Quinquenervia*, had orthotropic branch orientation (see S2 and  
433 S5). For LDMC, LA, WD and BT, phylogenetic signals were low to moderate (i.e.,  $0.29 \leq \lambda \leq 0.84$ ,  
434 Table 2). Phylogenetic signal of SLA was not significant ( $\lambda = 0$ , indicating phylogenetic  
435 independence). Branch orientation was the only trait for which we found a strong signal ( $D < 0$ ,  
436 Table 2).

437

#### 438 ***3.2 Spatial and temporal taxonomic turnover***

439 We found substantial species turnover either for spatial and temporal community composition along  
440 transects. Abundance-based and species-based spatial dissimilarities between communities ranged  
441 from 0.2 to 1 and both showed significant positive relationships with distance between pairs of  
442 communities along transects (Fig. 3). Temporal dissimilarity was higher at the edge when

443 considering species abundances, and significantly decreased toward forest interior either when  
444 considering species abundance or presence-absence (Fig. 3).

445

### 446 **3.3. Spatial variation in community mean trait values**

447 Overall, we found significant non-random patterns of community weighted-mean trait values for all  
448 measured traits (data from 2010, Fig. 4). When considering all trees, effect sizes of leaf area and  
449 SLA were lower than expected in edge communities, and increased with increasing distance from  
450 the edge. For all trees and small trees, these relationships were still significant when excluding the  
451 savanna species (*M. quinquenervia*), but not for large trees. For all size class, effect sizes of  
452 plagiotropy were lower than expected in edge communities and increased with distance from the  
453 edge, whether including *M. quinquenervia* or not (Fig. 4). On the contrary, for all size class, effect  
454 sizes of bark thickness were higher than expected in edge communities, and decreased with distance  
455 from edge. When excluding *M. quinquenervia*, this relationship was still significant only for small  
456 trees. Effect sizes of wood density were higher than expected in forest interior communities for all  
457 trees, and significantly increased with distance to edge for large trees (Fig. 4). Effect sizes of  
458 LDMC were lower than expected in forest interior communities for all trees, and higher than  
459 expected in edge communities for large trees.

460

### 461 **3.4. Spatial patterns of functional and phylogenetic diversity**

462 For each size class, effect sizes of functional diversity (FMPD) significantly increased with distance  
463 to edge with respect to NM1 (Fig. 5). In addition, edge communities showed higher functional  
464 clustering than expected under NM1. In contrast, effect sizes of phylogenetic diversity (PMPD) did  
465 not show significant variation with distance to edge. However, both edge and forest interior  
466 communities showed phylogenetic clustering with respect to NM1, except when considering only  
467 large trees. These trends were almost the same when excluding *M. quinquenervia*.

468

### 469 **3.5. Temporal variation in community mean trait values**

470 Effect sizes of temporal changes in community mean trait values between 2010 and 2018 ( $\Delta$ CWM)  
471 showed generally consistent but weakly significant patterns compared to the spatial changes  
472 observed in 2010 (i.e., compositional changes towards less drought- and fire-resistant trait values,  
473 S6). However, temporal variation in mean trait values were only significant when we included *M.*  
474 *quinquenervia* in the analysis, indicating no significant temporal shifts in community mean traits  
475 among forest species between the two censuses.

476

### 477 **3.6. Functional and phylogenetic temporal changes**

478 Effect sizes of temporal dissimilarity in functional composition ( $FD_{pw}$ ) within communities  
479 significantly decreased from the edge to the interior for large trees (Fig. 5, right panel), even when  
480 excluding *M. quinquenervia*, but this pattern was lost when considering all trees or small trees (Fig.  
481 5, left and center panels). However, temporal change in functional composition was lower than  
482 expected under NM2 for all trees in forest interior communities. For both all trees and large trees,  
483 we observed a decrease in effect sizes of temporal phylogenetic dissimilarity ( $PD_{pw}$ ) with increasing  
484 distance to edge. When excluding *M. quinquenervia*, this relationship was still significant for all  
485 trees. Finally, temporal phylogenetic dissimilarities were lower than expected under NM2 in forest  
486 interior communities for all class sizes.

487

## 488 **4. Discussion**

489 We evaluated spatio-temporal changes in functional and phylogenetic composition of tree  
490 communities with null models to infer the main processes driving tropical forest post-fire  
491 succession in anthropogenic savannas. In agreement with our expectations, our results revealed

492 coordinated shifts in functional and phylogenetic compositions during the succession, suggesting a  
493 primary role of environmental filtering related to fire and drought in young edge communities,  
494 followed by an increasing influence of light limitation. Furthermore, despite the short time interval  
495 studied (8 years), the observed temporal changes in community patterns were also partly consistent  
496 with our expectations, showing faster compositional changes at the beginning of the succession than  
497 in older communities of forest interior. Importantly, our study also suggests substantial contrasts in  
498 assembly processes operating on small and large trees during the succession.

499

#### 500 ***4.1. Fire and drought drive environmental filtering in edge communities***

501 Most functional studies investigating savanna-forest transitions have focused on comparing species  
502 groups from these two biomes (Maracahipes et al., 2018; Ratman et al., 2011). Our work indicates  
503 that forest communities located at the edge exhibit a particular set of traits associated with more  
504 drought- and fire-resistance strategies in comparison to forest interior communities, as recently  
505 suggested by recent studies (Cardoso et al. 2021; Flake et al. 2021). On our study site, the presence  
506 of the savanna specialist *M. quinquenervia* up to 40m inside the forest suggests a relatively low fire  
507 frequency and intensity during the last decades, which has allowed recent forest expansion (Ibanez  
508 et al. 2013c). However, the proximity of savanna entails dryer microclimatic conditions at the forest  
509 edge, notably during extreme drought periods (e.g., El Niño episodes), incurring higher probability  
510 of sporadic fire incursion (Brando et al., 2014; Cochrane, 2003; Hoffmann et al., 2012a; Ibanez et  
511 al., 2013a, Pausas et al., 2017). Our results suggest that sporadic fires may constrain species  
512 survival in young forest edge communities, favoring higher stem protection among small forest  
513 trees (i.e., higher bark thickness, Fig. 4), which is consistent with the study of Cardoso et al. (2021).  
514 Despite the limited resistance to fire of New Caledonian forest species (see Ibanez et al., 2013d),  
515 this indicates a significant role of fire-resistance in the establishment of species at the forest edge  
516 (see also Blanchard et al., 2020).

517 Interestingly, we found that orthotropic species were strongly favored in young edge communities,  
518 where plagiotropic species were almost absent (Fig. 4, S3). Plagiotropic growth could be disfavored  
519 at the savanna-forest boundary, because lower self-shading may increase leaf water loss and heat  
520 load in dryer conditions (Givnish, 1988). Furthermore, plagiotropic growth can increase fire  
521 damage for young trees, while orthotropic growth allows tree top to reach a size higher than flame  
522 height more quickly (Gignoux et al., 2016; Ratnam et al., 2011). In line with recent works (Charles-  
523 Dominique et al., 2018; Gignoux et al., 2016), our results thus suggest a substantial role of  
524 architectural traits in driving tree community assembly during forest expansion over savanna.

525 The observed smaller and more conservative leaves (lower SLA) at the beginning of the succession  
526 (i.e., in edge communities, Fig. 4) contrasts with other studies of tropical forest succession, which  
527 have found opposite trends in non-fire-prone landscapes (Craven et al., 2018; Lohbeck et al., 2013;  
528 Muscarella et al., 2016; Subedi et al., 2019). The specific conditions generated by the proximity of  
529 savanna may explain such differences. Indeed, higher drought intensity and potential fire incursion  
530 at the forest edge could favour smaller and thicker leaves, which limit water loss (Wright et al.,  
531 2017) and leaf flammability (Pausas et al., 2017). Nonetheless, the absence of strong variations in  
532 wood density and LDMC during succession, traits known to positively correlate to drought  
533 resistance (Chave et al., 2009; Markesteijn et al., 2011), does not fully support this hypothesis.  
534 Another factor potentially explaining the prevalence of conservative leaf strategies in young edge  
535 communities is the lower nutrient availability in savanna (Flake et al. 2021; Geiger et al., 2011;  
536 Rossatto et al., 2013; Silva et al., 2013). In addition, this result could reflect a trade-off in leaf  
537 biomass allocation, as higher biomass per leaf area can improve light-capture in high-light  
538 conditions of the forest edge (Poorter et al., 2009), which is also consistent with our expectations.

539 We found a marked increase in functional diversity from edge to forest interior, with the edge  
540 communities being both functionally and phylogenetically clustered with respect to null  
541 expectations (Fig. 4). This indicates a stronger influence of environmental filtering during the early  
542 succession, in accordance with some studies of tropical forest succession (Letcher et al., 2012;

543 Lohbeck et al., 2014), but in contrast with some others (Craven et al., 2018; Muscarella et al.,  
544 2016). These results comfort our hypothesis that the specific environmental conditions related to the  
545 post-fire context entails strong filtering on species establishment at the beginning of the succession.  
546 Among forest species, spatial variations in mean traits were generally stronger for small trees than  
547 for large trees (Fig. 4), suggesting that they underwent stronger shifts in limiting factors between  
548 forest edge and interior. In addition, small trees tend to be more phylogenetically clustered than  
549 under null expectations all along the succession, while the phylogenetic structure of large trees did  
550 not deviate from random. This supports that the dynamics of small trees is more constrained by  
551 environmental filtering than that of large trees. As large trees can represent an older successional  
552 cohort (Baldeck et al., 2013; Letcher, 2010), this may reflect a shift from abiotic to biotic  
553 constraints during ontogeny, with stronger neighborhood interactions among large and older canopy  
554 trees, as revealed by previous works (Fang et al., 2019; Lasky et al., 2015; Swenson et al., 2007).

555 Despite the short time interval considered in this study (8 yrs), our results showed significant  
556 contrasts regarding temporal changes in composition within communities. The temporal  
557 dissimilarity within communities was higher in edge communities than in forest interior (Fig. 3),  
558 indicating faster taxonomic turnover at the beginning of the succession. Our results also indicate  
559 faster temporal changes in both functional and phylogenetic composition of edge communities than  
560 in forest interior (Fig. 6). However, these changes did not deviated from the null expectations and  
561 we did not find any temporal changes in mean trait values of forest species between the two census  
562 (see S6), contrary to our expectation. Therefore, although the turnover in species taxonomic,  
563 functional and phylogenetic composition was faster at the edge, there were no successional shift in  
564 species function during the studied time interval. These results may reflect the partial influence of  
565 stochastic demography among forest species, as well as the influence of drought and sporadic fires  
566 on tree recruitment at the edge. Observing a successional shift in species functions in edge  
567 communities may thus require longer studies and/or strict absence of fire influence. The specific  
568 post-fire environment could thus incur slower successional dynamics compared to fire-free



569 contexts, as recently suggested by Flake et al. (2021). It worth noting that no *M. quinquenervia*  
570 were recruited in forest communities, supporting a rapid exclusion of savanna species after forest  
571 expansion, as suggested by other studies in Africa and South America (Charles-Dominique et al.,  
572 2018; Geiger et al., 2011).

573

#### 574 **4.2. Light limitation and slow temporal changes in forest interior communities**

575 The absence of remnant savanna-specialist trees (*M. quinquenervia*) in forest interior communities  
576 (i.e., > 50m from the edge) indicates that this part of the forest is older than edge communities, and  
577 thus represents a latter successional stage (Ibanez et al., 2013b). Our findings indicate that species  
578 with larger and more acquisitive leaves were favored in these older communities of forest interior  
579 (Fig. 4). This can be due to moister, cooler micro-climate (Ibanez et al., 2013a), and probably higher  
580 soil fertility in forest interior. In addition, thinner and larger leaves also maximize light capture  
581 under shade conditions, providing a competitive advantage in low-light environment of forest  
582 interior, where light-demanding species tend to be excluded (Chazdon, 2008; Givnish, 1987; Pinho  
583 et al., 2018; Poorter et al., 2009). Thus, our study supports the key role of the sharp light gradient  
584 running from savanna to forest interior in shaping the functional composition of tree communities  
585 during forest expansion (Cardoso et al., 2016; Charles-Dominique et al., 2018; Ratnam et al., 2011).  
586 This pattern is also in agreement with the ‘productivity filtering hypothesis’, which predicts that  
587 increasing water and nutrient availability and decreasing light availability drives a slow-to-fast shift  
588 in species strategies along succession (Buzzard et al., 2015).

589 Next, our results showed a strong shift in species architecture, with an increase in plagiotropic  
590 branch orientation from the edge to forest interior, which also supports the hypothesis of increasing  
591 influence of light-limitation during the succession. Both orthotropic and plagiotropic species  
592 occurred in forest interior (see S3). Such alternative growth strategies could be associated with  
593 different forest strata. Canopy species could have more vertical growth to reach the light, while

594 understory species may have more horizontal growth, hence limiting self-shading and improving  
595 light interception (Poorter et al., 2006; Subedi et al., 2019). Large trees had higher wood density in  
596 forest interior than at the edge, suggesting the need of denser wood to support taller canopy trees  
597 with longer life-span when light is more limiting (Maracahipes et al., 2018; Poorter et al., 2010).

598 We found no functional or phylogenetic overdispersion in forest interior communities, as it would  
599 be expected under an overwhelming influence of limiting similarity (Letcher et al., 2012; Mayfield  
600 and Levine, 2010). On the contrary, functional and diversity of forest interior communities did not  
601 deviate from random and phylogenetic diversity tended to be clustered (Fig. 5). Moreover,  
602 functional and phylogenetic temporal dissimilarities in forest interior were lower than expected  
603 under the null model (Fig. 6), supporting that temporal change in species strategies slows down  
604 during the succession (Cequinel et al., 2018; Fang et al., 2019; Swenson et al., 2012). Together,  
605 these patterns could reflect an increasing influence of asymmetric competition for light (i.e.,  
606 competitive dominance of shade-adapted species), as suggested by other studies (Buzzard et al.,  
607 2015; Craven et al., 2018). Such phylogenetic clustering and slow temporal changes may also  
608 reflect constraints operating on unmeasured traits. For instance, reproductive and seed traits could  
609 be more constrained in shadier conditions of old-growth forest interior (Lasky et al., 2015; Swenson  
610 et al., 2012). Likewise, Cavender-Bares et al. (2009) suggested that generalist herbivore pressure  
611 could lead to phylogenetic clustering if defense strategies are conserved through evolutionary  
612 history. Nonetheless, the relative influence of specific assembly processes cannot be disentangled  
613 here, as environmental filtering and biotic interactions can both lead to phylogenetic convergence  
614 and can jointly interact to shape community patterns (Kraft et al., 2015; Mayfield and Levine,  
615 2010).

616

## 617 **5. Conclusion**

618 By analyzing spatial and temporal variations in functional and phylogenetic composition of tree  
619 communities, we inferred the main factors driving tropical forest post-fire succession in  
620 anthropogenic savannas. In accordance with classical literature on tropical forests, our study  
621 showed that increasing light limitation is a primary factor of post-fire succession. However, our  
622 work also underlined a substantial role of fire and drought in filtering forest species establishing in  
623 young edge communities. Importantly, such filtering operates on distinct functional dimensions,  
624 involving leaves, stem and tree architecture, entailing a functional trajectory differing from typical  
625 tropical forest succession. This strongly suggests that, in the specific post-fire context, tropical  
626 forest recovery relies on the establishment of forest species with a particular set of traits. The  
627 limited rate of temporal change in functional and phylogenetic composition we found also suggests  
628 that forest successional dynamics may be slower than in fire-free contexts. Our study improve the  
629 understanding of the ecological processes driving tropical forest recovery in anthropogenic fire-  
630 prone landscapes and should help to better restore forest in these areas.

631

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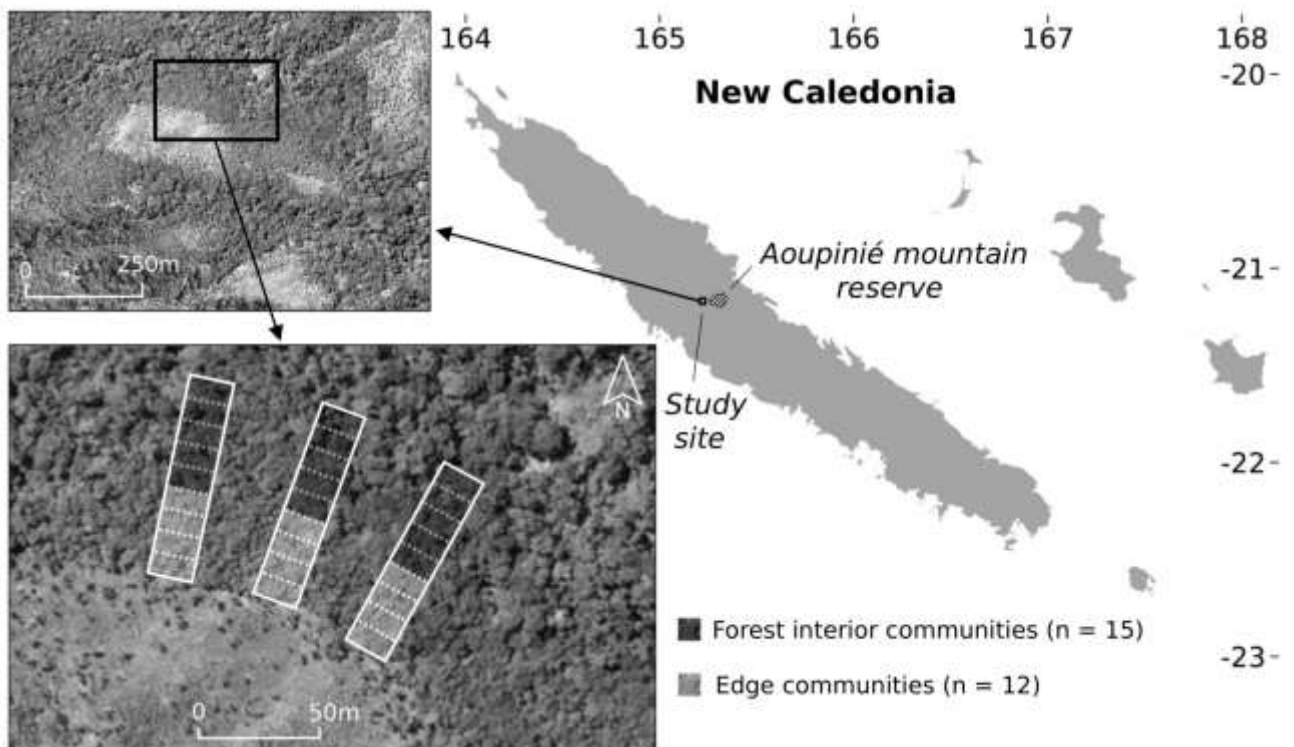
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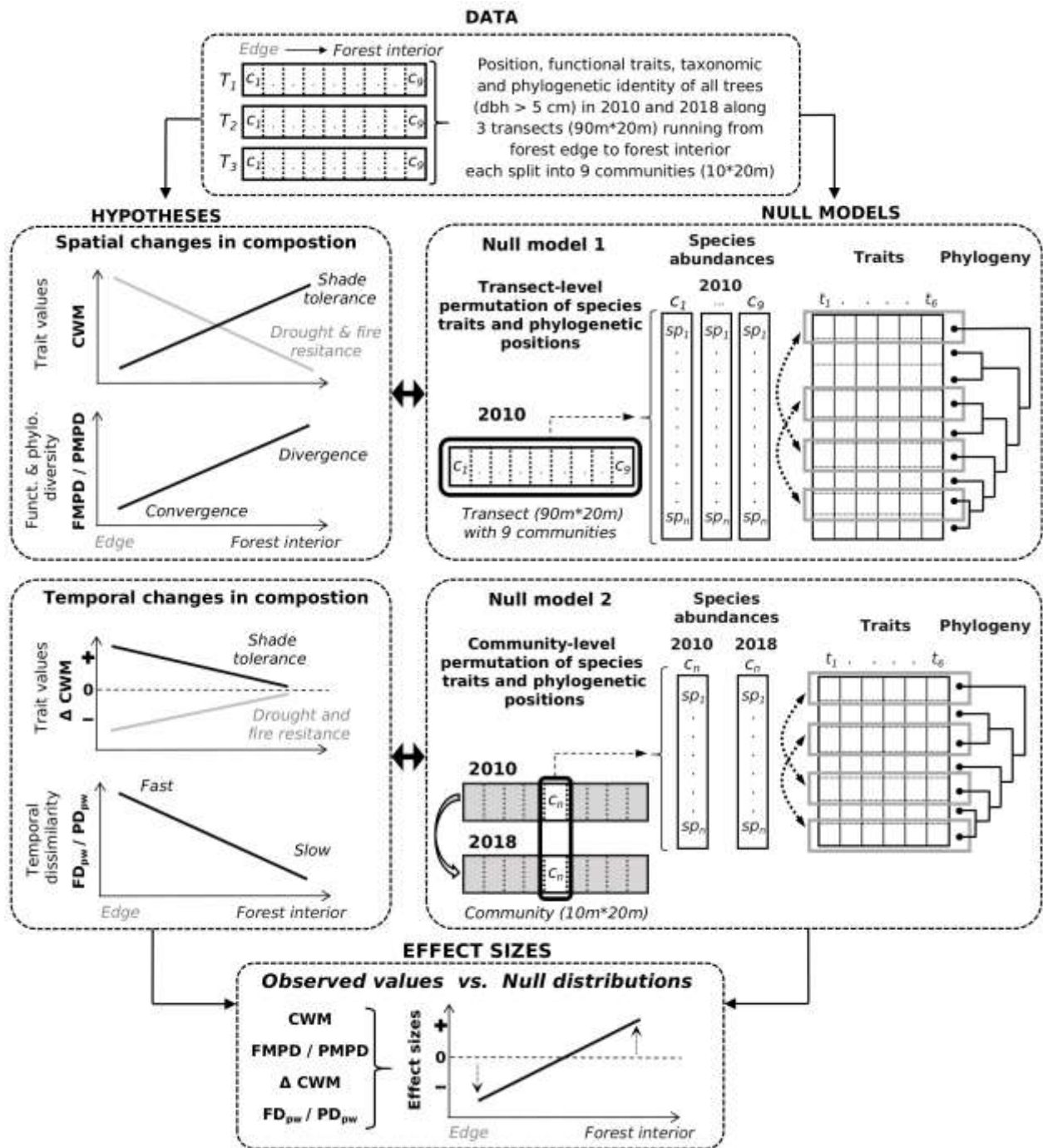
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640 Figure 1. Map and aerial photographs showing the location of the studied site and the position of  
 641 the three established transects (20×90m) running from savanna-forest edge to forest interior, on the  
 642 west side of the Aoupinié mountain reserve, in New Caledonia (south-west Pacific). Dotted lines  
 643 represent transect subdivisions corresponding to different successional communities (20×10m,  
 644 n=27). Communities located between the edge and 40m inside the forest are considered as edge  
 645 communities, while communities located at more than 40m from the edge are considered as forest  
 646 interior communities.

647



648 Figure 2. Hypotheses tested and associated null models. Null model 1 (NM1), permutation of  
 649 species attributes (i.e., trait values and phylogenetic position) between all species occurring in 2010  
 650 within each transect, was used to test for spatial changes in species trait values and divergence or  
 651 convergence with respect to transect-level composition. Null model 2 (NM2), permutation of  
 652 species attributes between all species occurring in either 2010 or 2018 within each community, was  
 653 used to test for temporal change in mean trait values and functional and phylogenetic dissimilarity  
 654 between species composition in 2010 and 2018. Species attributes were always permuted jointly.

655 Effect sizes were computed to compare the observed values of each metric with their null  
656 distributions.

Traits	Fire-resistance	Drought-resistance	Shade-tolerance	Other important functions
Leaf area (LA)		↘ (Markesteijn et al. 2011; Moles 2018; Wright et al., 2017)	↗ (Díaz et al. 2016; Givnish, 1987; Moles 2018; Pierce et al. 2013)	Gas exchange surface (Moles 2018)
Leaf dry matter content (LDMC)	↗ (Mason et al. 2016)	↗ (Markesteijn et al., 2011)		Resources conservation (Hodgson et al., 2011)
Specific leaf area (SLA)	↘ (Pausas et al. 2017)	↘ (Moles, 2018; Poorter et al. 2009)	↗ (Pinho et al., 2018)	Resources acquisition, Vulnerability to herbivory (Díaz et al. 2016; Markesteijn et al. 2011; Moles 2018, Poorter et al. 2009; Wright et al. 2004)
Orthotropy	↗ (Charles-Dominique et al., 2018; Gignoux et al., 2016)		↘ (Givnish, 1988)	
Plagiotropy	↘ (Charles-Dominique et al., 2018; Gignoux et al., 2016)		↗ (Givnish 1988; Küppers, 1989; Poorter et al. 2006)	
Wood density (WD)	↗ (Brando et al. 2012)	↗ (Chave et al. 2009; Poorter et al. 2010)	↗ (Markesteijn et al. 2011)	Mechanical support (Chave et al. 2009; Moles 2018)
Bark thickness (BT)	↗ (Brando et al. 2012; Rosell 2016; Pausas, 2015)	↗ (Poorter et al. 2014)		Protection from herbivory and mechanical injuries (Rosell 2016)

657

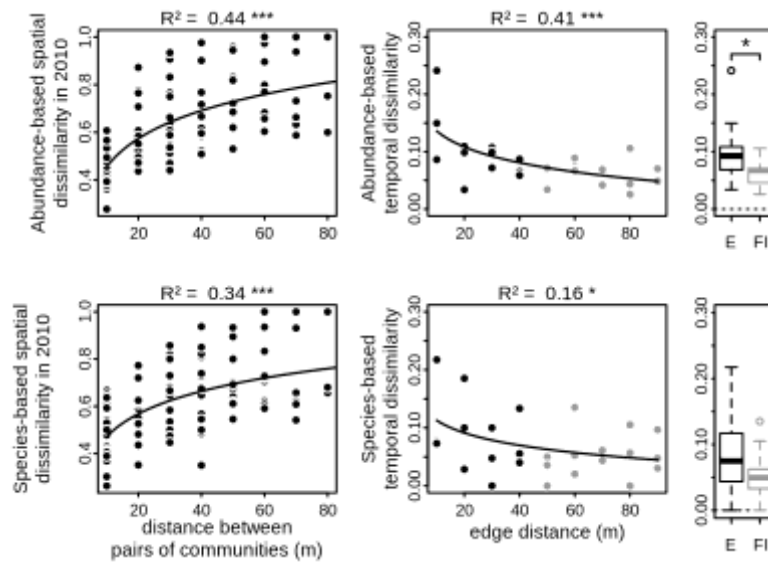
658 Table 1. Correlations between measured functional traits and their related functions regarding the  
659 main species functions expected to play a role in community assembly during forest succession,  
660 based on literature (references are listed in the table). Upward or downward arrows indicate positive  
661 or negative correlation between trait values and related functions, respectively. Other important  
662 functions related to the measured traits are also listed in the right column.

663

Trait	LA	LDMC	SLA	Branch orientation	WD	BT
Pagel's $\lambda$	0.29*	0.84***	0	.	0.46***	0.34*
<i>D</i>	.	.	.	-0.70***	.	.

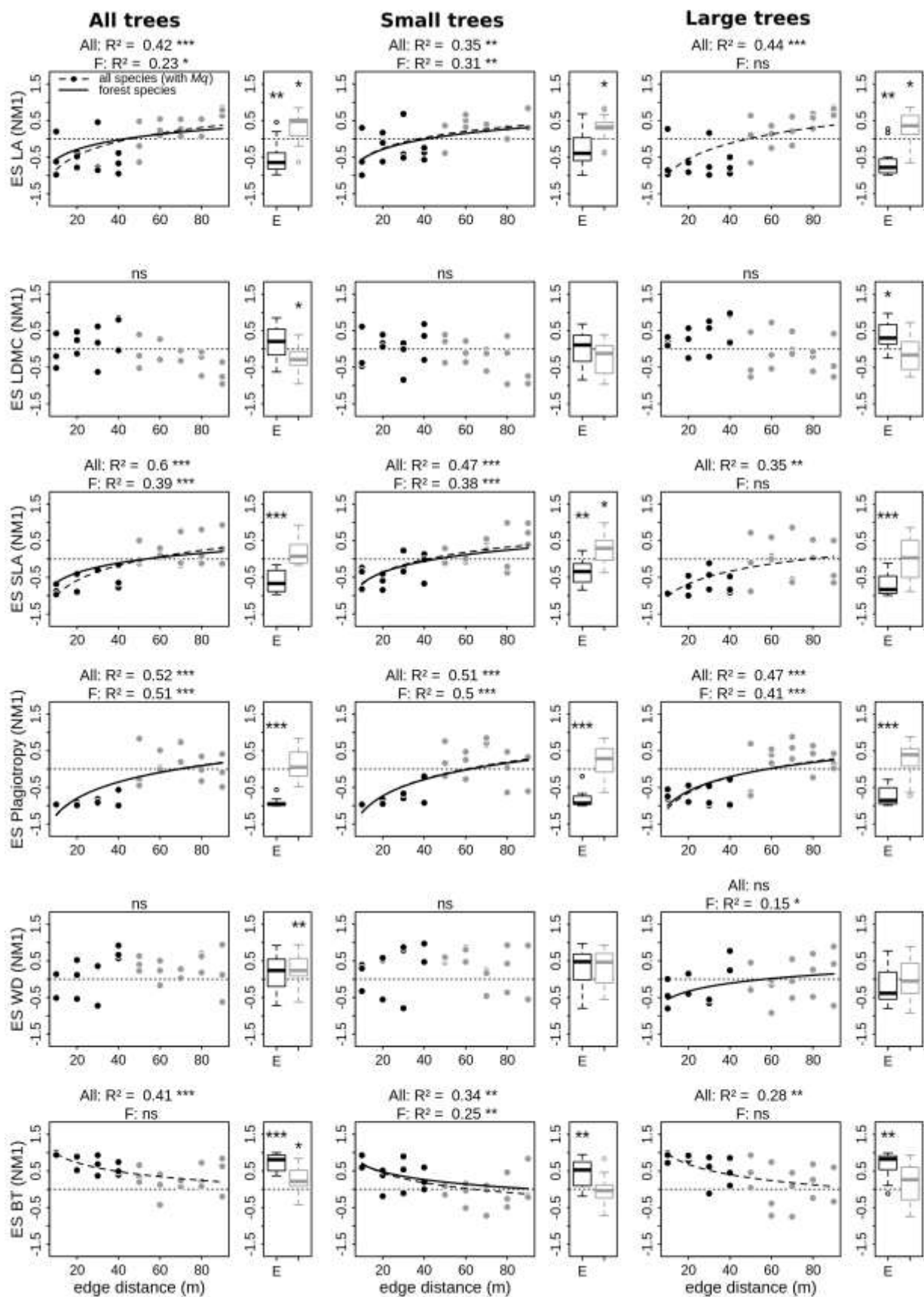
664

665 Table 2. Phylogenetic signal (Pagel's  $\lambda$  and *D* values) of six measured traits (leaf area, LA; leaf dry  
666 matter content, LDMC; specific leaf area, SLA; Branch orientation; wood density, WD; bark  
667 thickness ratio, BT) for 89 species. Signal significance were obtained with a permutation test (\*: p-  
668 value < 0.05; \*\*: p-value < 0.01; \*\*\*: p-value < 0.001).



669 Figure 3. Spatial and temporal changes in community taxonomic composition along transects. Left  
670 panels show the relationships between the abundance-based and species-based (i.e., presence-  
671 absence) Bray-Curtis dissimilarities and the distance between pairs of communities of each transect.  
672 The savanna species *M. quinquenervia* was excluded from these analyses. Right panels show the  
673 relationships between abundance-based and species-based temporal dissimilarity between the two  
674 censuses in 2010 and 2018 within each community and distance to forest edge. For the significant  
675 relationships, the curves indicates the predictions of the linear model (model were fitted using log-  
676 transformed distance to edge) and R-squared is reported (ns: p-value > 0.05, \*: p-value < 0.05; \*\*: p-  
677 value < 0.01; \*\*\*: p-value < 0.001). Black and grey points indicate edge and forest interior  
678 communities, respectively. For temporal dissimilarity, boxplots show differences between edge  
679 (black) and forest interior (grey) communities, tested using two-sample Wilcoxon signed rank tests  
680 (ns: p-value > 0.05, \*: p-value < 0.05; \*\*: p-value < 0.01; \*\*\*: p-value < 0.001).

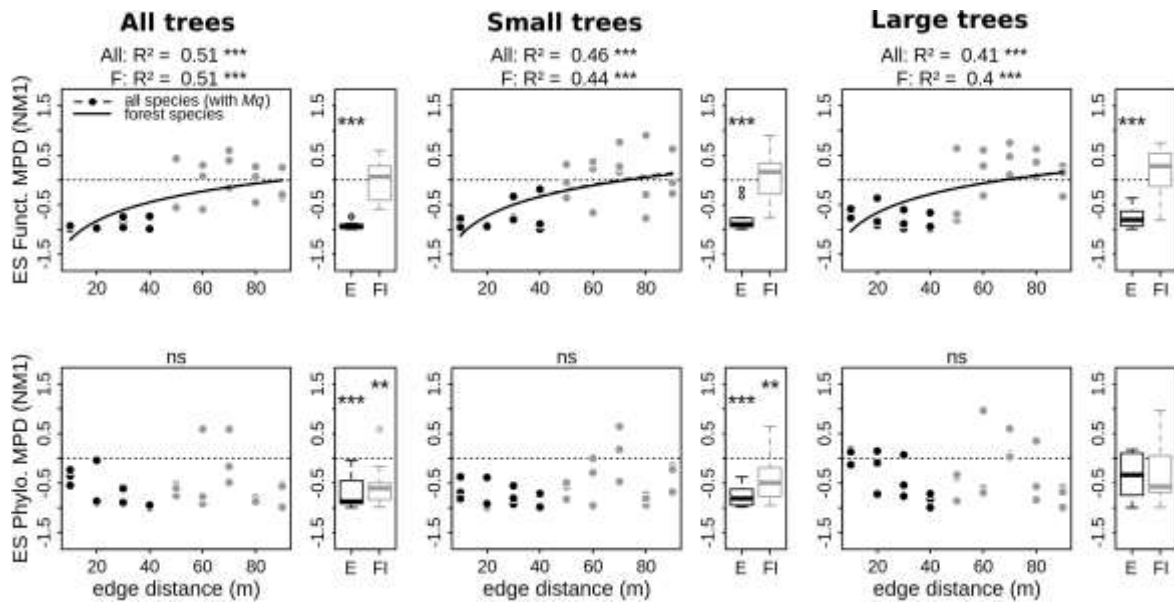




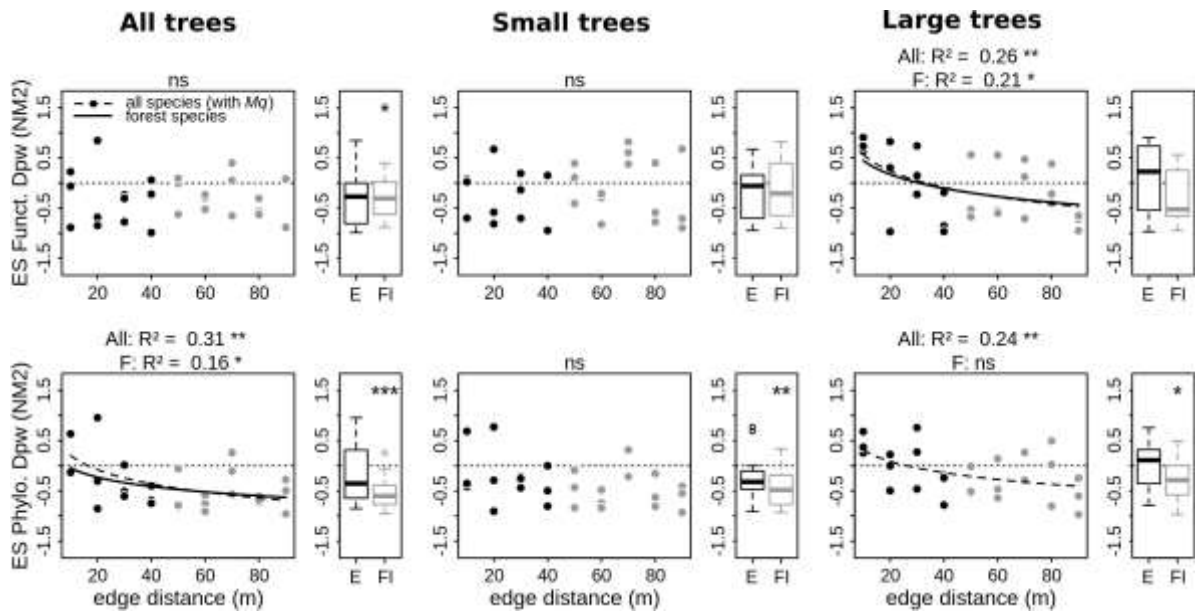
681 Figure 4. Relationship between effect size (ES) of community weighted mean trait (CWM) and  
 682 distance from edge (data from 2010). ES were obtained by comparing observed values of CWM  
 683 from their null distribution under NM1 (i.e., random community composition with respect to

684 species attributes at the transect level). Positive (or negative) ES values indicate that CWM are  
685 higher (or lower) than expected in NM1, respectively. For significant relationships, curves indicate  
686 the predictions of linear models (models were fitted using log-transformed distance to edge but  
687 predictions are plotted on a regular scale, resulting in non-linear relationships) and R-squared are  
688 reported. Black and grey points indicate edge and forest interior communities, respectively.  
689 Relationships were tested either with all species (dashed curves) and with only forest species (by  
690 excluding *M. quinquenervia*, solid curves). Boxplots show divergences of ES of CWM from zero  
691 for all edge communities (black) and all forest interior communities (grey), tested using one-sample  
692 Wilcoxon signed rank tests. (ns: p-value > 0.05, \*: p-value < 0.05; \*\*: p-value < 0.01; \*\*\*: p-value  
693 < 0.001).

694

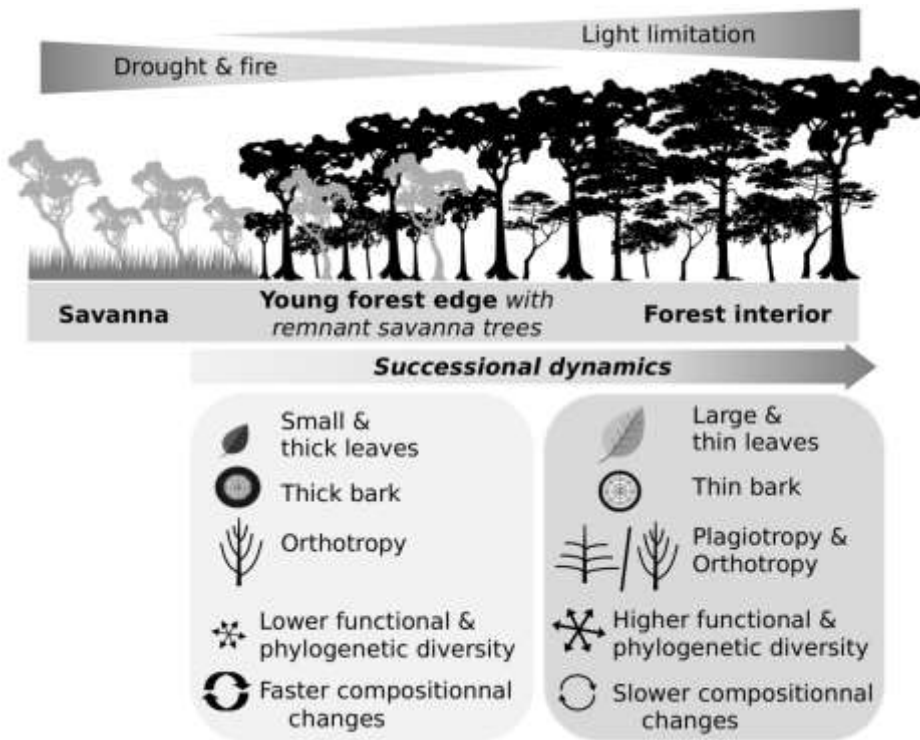


695 Figure 5. Relationship between effect sizes (ES) of the abundance-weighted functional and  
696 phylogenetic mean pairwise distances (MPD) and distance from edge (data from 2010). ES were  
697 obtained by comparing observed values of MPD from their null distribution under NM1 (i.e.,  
698 random community composition with respect to species attributes at the transect level). Positive, or  
699 negative ES values indicate that MPD are higher, or lower than expected in NM1, respectively. For  
700 significant relationships, curves indicate the predictions of linear models (models were fitted using  
701 log-transformed distance to edge but predictions are plotted on a regular scale, resulting in non-  
702 linear relationships) and R-squared are reported. Black and grey points indicate edge and forest  
703 interior communities, respectively. Relationships were tested either with all species (solid curves)  
704 and with only forest species (by excluding *M. quinquenervia*, dashed curves). Boxplots show  
705 divergences of ES of MPD from zero for all edge communities (black) and all forest interior  
706 communities (grey), tested using one-sample Wilcoxon signed rank tests. (ns: p-value > 0.05, \*: p-  
707 value < 0.05; \*\*: p-value < 0.01; \*\*\*: p-value < 0.001).



708

709 Figure 6. Relationship between effect sizes (ES) of functional and phylogenetic mean pairwise  
 710 dissimilarity ( $D_{pw}$ ) and distance from edge (change in composition between 2010 and 2018). ES  
 711 were obtained by comparing observed values of  $D_{pw}$  from their null distribution under NM2 (i.e.,  
 712 random temporal change in composition with respect to species attributes at the community level).  
 713 Positive, or negative ES values indicate that  $D_{pw}$  are higher, or lower than expected in NM2,  
 714 respectively. For significant relationships, curves indicate the predictions of linear models (models  
 715 were fitted using log-transformed distance to edge but predictions are plotted on a regular scale,  
 716 resulting in non-linear relationships) and R-squared are reported. Black and grey points indicate  
 717 edge and forest interior communities, respectively. Relationships were tested either with all species  
 718 (solid curves) and with only forest species (by excluding *M. quinquenervia*, dashed curves).  
 719 Boxplots show divergences of ES of  $D_{pw}$  from zero for all edge communities (black) and all forest  
 720 interior communities (grey), tested using one-sample Wilcoxon signed rank tests. (ns: p-value >  
 721 0.05, \*: p-value < 0.05; \*\*: p-value < 0.01; \*\*\*: p-value < 0.001).



722

723 Graphical abstract. Schematic representation of the successional pathway operating during forest  
 724 recovery in anthropogenic savannas of New Caledonia. Contrasts in functional and phylogenetic  
 725 composition, diversity, as well as in temporal change in composition between forest edge  
 726 communities in forest interior communities are indicated. The influence of drought and fire favours  
 727 species with small and thicker leaves, thicker bark and orthotropic growth in edge communities,  
 728 while increasing light-limitation favours species with large and thinner leaves, thinner bark as well  
 729 as both plagiotropic and orthotropic growth. Functional and phylogenetic diversity increases during  
 730 succession, but the rate of temporal changes in composition slows down in forest interior.

731