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

2 **anthropogenic savannas**

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4 Grégoire Blanchard[1,2,3], Thomas Ibanez[1], François Munoz[4], David Bruy[1,3], Christelle Hely[5,6],

5 Jérôme Munzinger[1] and Philippe Birnbaum[1,3,7]

6 [1]AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

7 [2]Institut Agronomique neo-Caledonien (IAC), Equipe Sol & Vegetation (SolVeg), Nouméa, New

8 Caledonia

9 [3]AMAP, IRD, Herbier de Nouvelle Calédonie, Nouméa, New Caledonia

10 [4]University Grenoble-Alpes, Laboratoire Interdisciplinaire de Physique (LIPhy), Saint-Martin-

11 d'Hères, France

12 [5]ISEM, Université Montpellier, CNRS, EPHE, IRD, Montpellier, France

13 [6]EPHE, PSL University, Paris, France

14 [7]CIRAD, UMR AMAP, F 34398, Montpellier, France

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16 Corresponding author: Grégoire Blanchard.

17 E-mail address: gregoire.blanchard@ird.fr

18 Postal address: Centre IRD de Nouméa, B.P. A5, 98848 Nouméa, Nouvelle-Calédonie

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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.

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).

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

2. Material and Methods

2.1. Study site and data collection

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

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

In 2010, along each transects, all trees with a diameter at breast height (DBH) ≥ 5cm were identified at the species level, tagged, and mapped (see Ibanez et al., 2013b), resulting in a total of 1435 individuals recorded in the forest part of the three transects (478 on average). In 2018, each transect was re-surveyed following the exact same protocol. During this second census, 118 trees that were previously recorded in 2010 were dead, and 126 new trees (DBH ≥ 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 200m² 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

2.4. Species traits

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

We measured three leaf traits on five leaves per individual and five individuals per species. We collected healthy and sun-exposed leaves (or leaves most exposed to direct sunlight for understory species). For each species, leaves were collected from adult trees located at different distance from the edge, in order to account as much as possible for potential intraspecific variation. For compound leaves, we considered a leaflet as the laminar unit. Petioles and petiolules were removed from leaves before measurement. We measured Leaf Area (LA, the area of a leaf in cm²), Specific Leaf Area (SLA, the leaf area per dry mass in $cm^2 \times g^{-1}$), and Leaf Dry-Matter Content (LDMC the leaf dry mass per fresh mass in $mg \times g^{-1}$). LA values were log-transformed to correct for non-normality prior to analysis. We also collected two stem traits at breast height (i.e., 1.3 m above ground): Wood Density (WD) by collecting one wood sample (5.15mm diameter core) per individual on five individuals per species, and relative Bark Thickness (i.e., relative to stem radius, BT) by systematically measuring bark thickness at two opposite points on all individuals. Trait data were partially completed with data from the NC-PIPPN database (for 44 species for leaf traits, i.e., 50% of the dataset, and for 66 species for WD, i.e., 75% of the dataset) in which traits were collected in the same region and following the same standardized protocols (Blanchard et al., 2019, 2020; Ibanez et al., 2017). Branch orientation was determined for each species in the field (following methods described by Barthélémy and Caraglio, 2007). Species with horizontal branch growth and bilateral symmetry were denoted as "plagiotropic", and species with vertical branch growth and 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 ΔCWM, 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 ΔCWM 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 λ (Pagel 1999), which is robust to polytomies (Molina-Venegas and Rodríguez,

321 2017), using the phytools R package (Revell, 2012). For Pagel's λ, 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 phylognetic composition of communities

356 (CWM, FMPD, PMPD) or temporal changes in this composition (ΔCWM, 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 ΔCWM, FD_{pw} and PD_{pw}. We interpreted non-random variation in

389 ΔCWM 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, ΔCWM

391 should shift towards less fire- and drought-resistant trait values in edge communities (Fig. 2). We

392 interpreted higher or lower FD_{pw} and 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 FD_{pw} and 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

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

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 (5cm ≤ DBH < 10cm, 45.7% of individuals) and

420 large trees (DBH ≥ 10cm, 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., LA < 92%, SLA < 98%, and 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

3.5. Temporal variation in community mean trait values

470 Effect sizes of temporal changes in community mean trait values between 2010 and 2018 (ΔCWM)

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

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

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

638   **References**

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Figures and tables
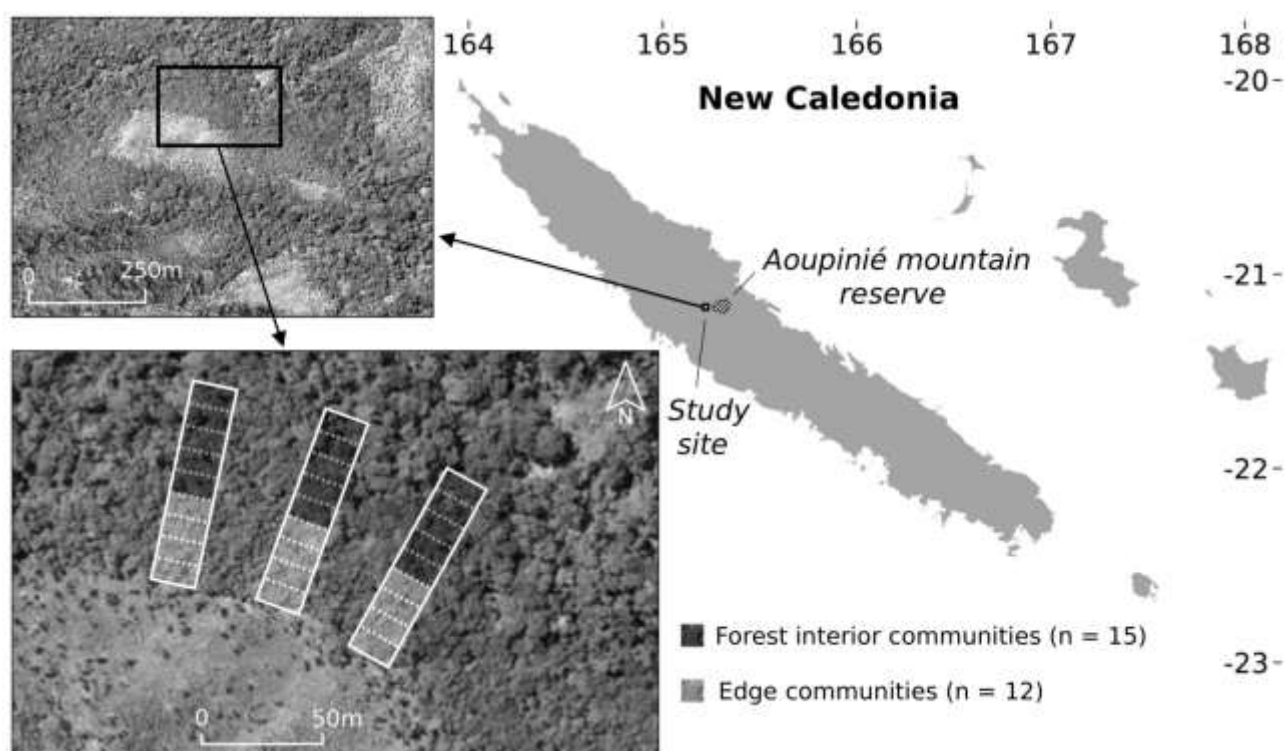
640 Figure 1. Map and aerial photographs showing the location of the studied site and the position of

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.

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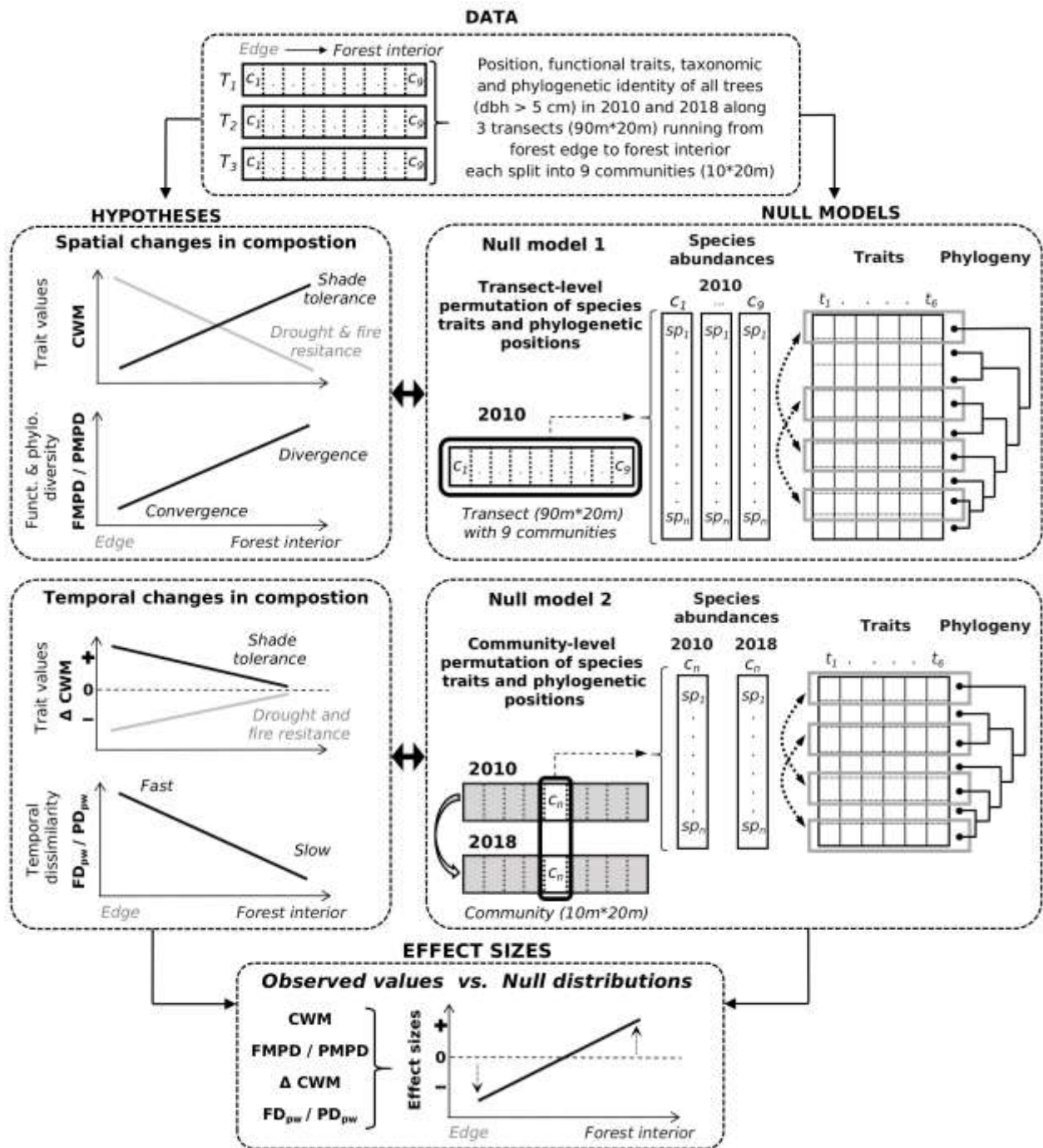
648 Figure 2. Hypotheses tested and associated null models. Null model 1 (NM1), permutation of

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

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

663

Trait	LA	LDMC	SLA	Branch orientation	WD	BT
Pagel's λ	0.29*	0.84***	0	.	0.46***	0.34*
D	.	.	.	-0.70***	.	.

664

665 Table 2. Phylogenetic signal (Pagel's λ 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).
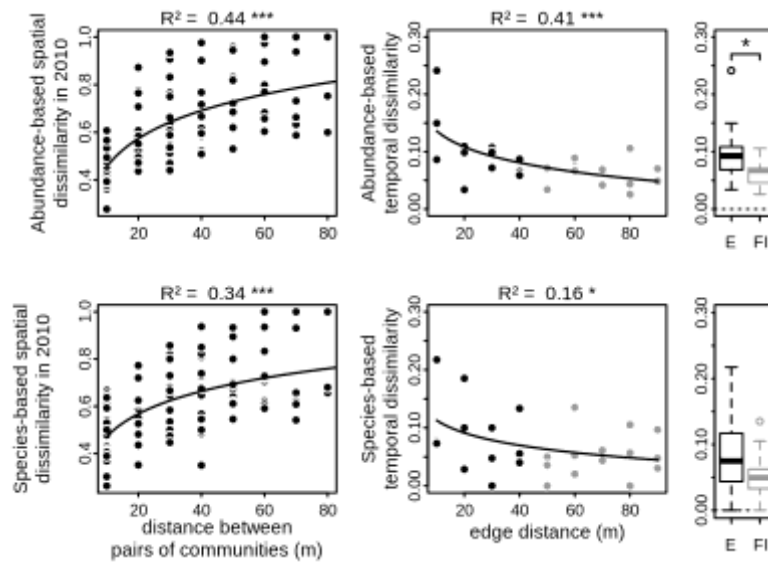
Figure 3. Spatial and temporal changes in community taxonomic composition along transects. Left panels show the relationships between the abundance-based and species-based (i.e., presence-absence) Bray-Curtis dissimilarities and the distance between pairs of communities of each transect. The savanna species *M. quinquenervia* was excluded from these analyses. Right panels show the relationships between abundance-based and species-based temporal dissimilarity between the two censuses in 2010 and 2018 within each community and distance to forest edge. For the significant relationships, the curves indicates the predictions of the linear model (model were fitted using log-transformed distance to edge) and R-squared is reported (ns: p-value > 0.05, *: p-value < 0.05; **: p-value < 0.01; ***: p-value < 0.001). Black and grey points indicate edge and forest interior communities, respectively. For temporal dissimilarity, boxplots show differences between edge (black) and forest interior (grey) communities, tested using two-sample Wilcoxon signed rank tests (ns: p-value > 0.05, *: p-value < 0.05; **: p-value < 0.01; ***: p-value < 0.001).
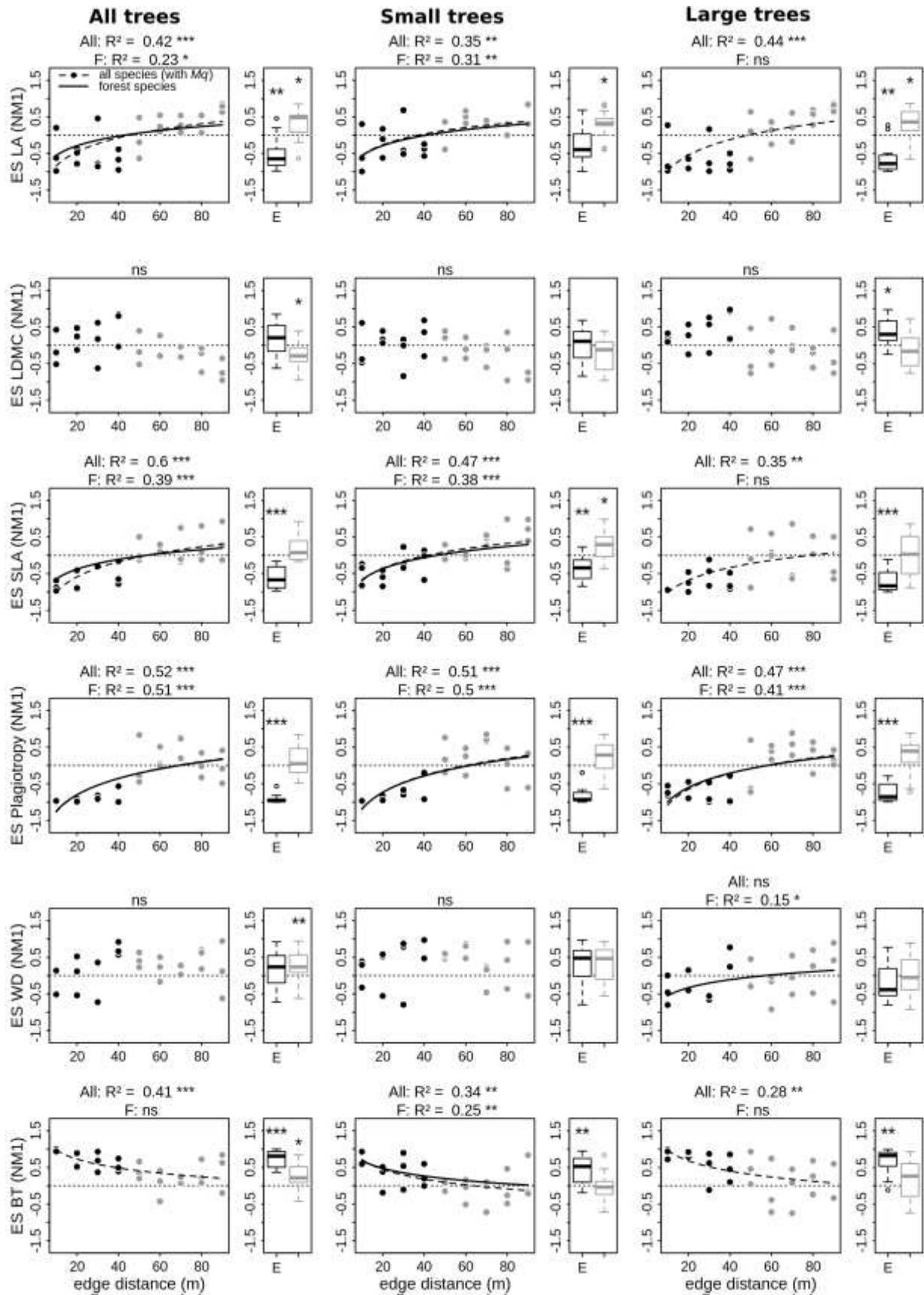
681   Figure 4. Relationship between effect size (ES) of community weighted mean trait (CWM) and

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
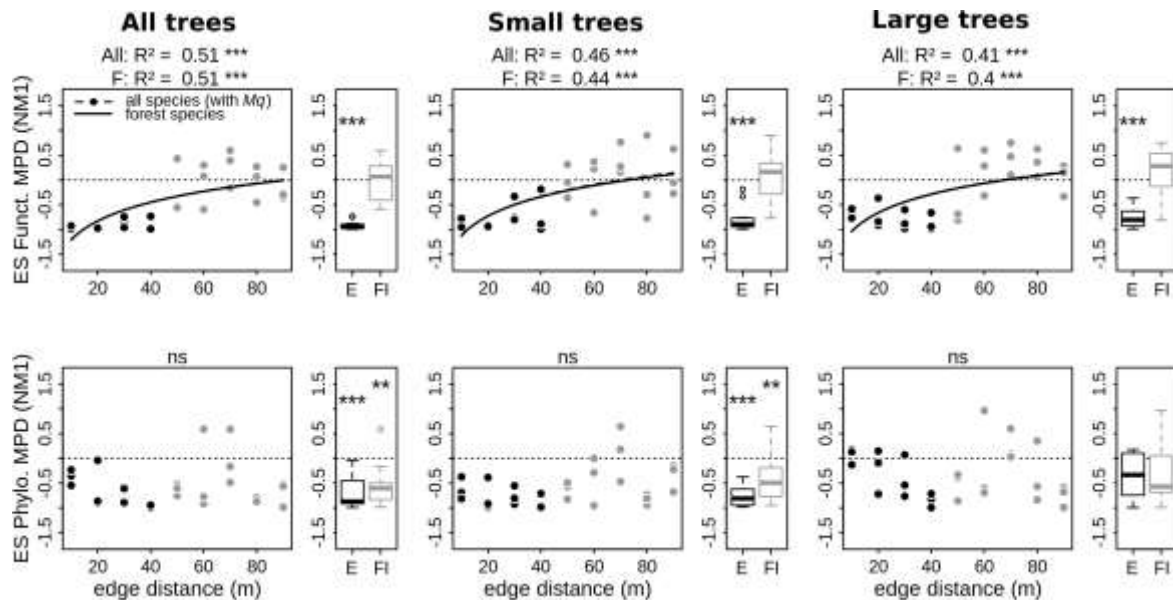
693 < 0.001).

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

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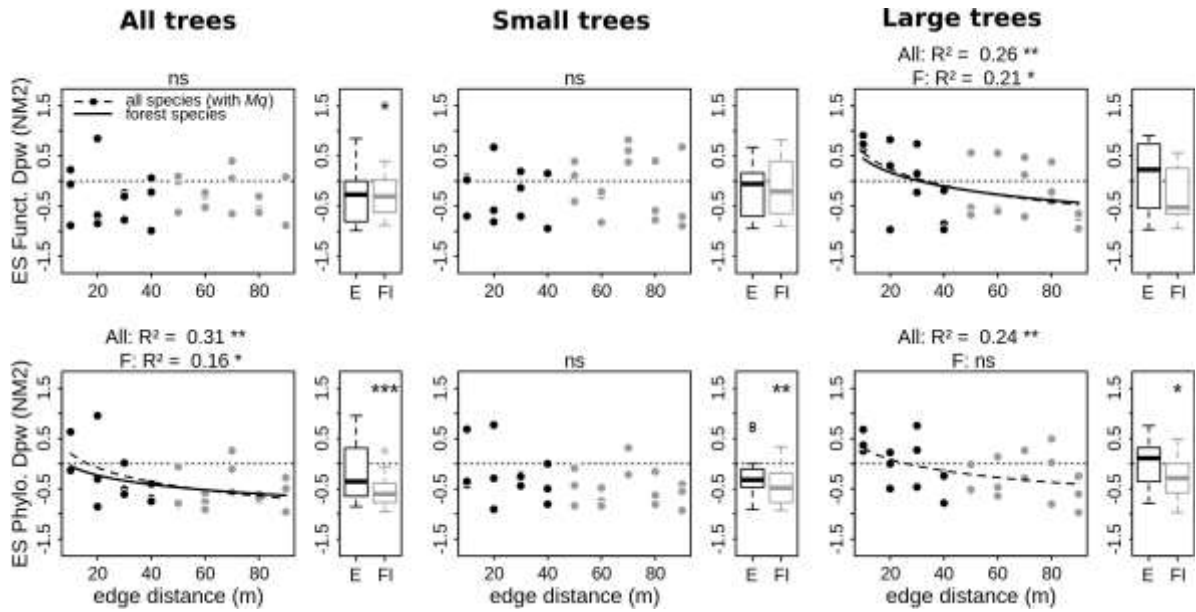
Figure 6. Relationship between effect sizes (ES) of functional and phylogenetic mean pairwise dissimilarity (D_{pw}) and distance from edge (change in composition between 2010 and 2018). ES were obtained by comparing observed values of D_{pw} from their null distribution under NM2 (i.e., random temporal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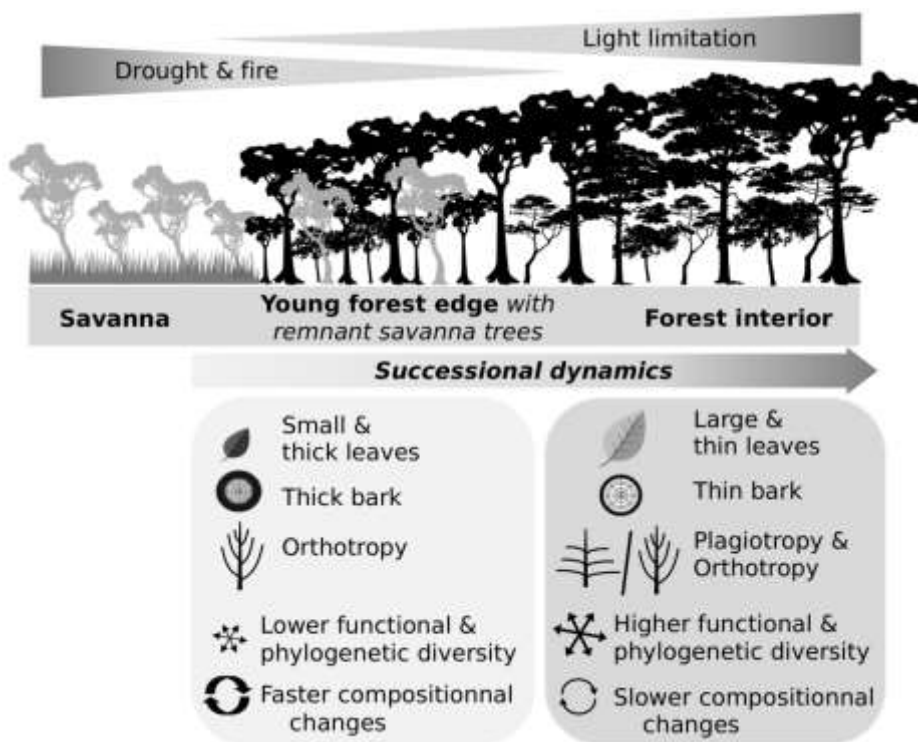
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723 Graphical abstract. Schematic representation of the successional pathway operating during forest

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.

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