

Manuscript Details

Manuscript number	PPEES_2017_83_R2
Title	Focusing on individual species reveals the specific nature of assembly mechanisms in a tropical dry-forest.
Article type	Research Paper

Abstract

We employed an individual-species approach based on the plant's eye perspective to disentangle the effects of individual species on community assembly in a dry tropical forest of southern Ecuador. We completely mapped a forest plot of 9 ha, and measured several functional traits (leaf area, specific leaf area, wood density, seed mass and maximum height) for tree and shrub species. To account for stochastic and habitat filtering effects, we fitted spatial point processes for the 23 more abundant species in the plot, which confirmed that all species responded to plot scale habitat filtering and 14 were dispersal-limited. We tested the hypothesis that facilitative interactions would be prevalent in this dry forest. For this, we compared the distribution of taxonomic (TD), functional (FD) and phylogenetic (PD) diversity in the neighborhood of the studied species with the diversity expected under a null model combining habitat filtering and stochastic assembly. We found that in the fine spatial scales where species interactions are expected to occur (i.e., neighborhoods of 1-20 m) eight species did not show any significant pattern for TD, FD or PD. Eleven species showed evidences of facilitation (i.e., accumulated more TD than expected) but in some cases the facilitated neighborhoods had more FD or PD than expected, suggesting the joint effect of facilitation and competition based on niche differences. One species showed less TD than expected, accompanied by lower FD and higher PD, suggesting competition based on fitness differences. Our study shows that in this dry tropical forest, where abiotic stress is prevalent, the assembly of diversity is controlled by environmental heterogeneity and both facilitative and competitive biotic processes, all of them acting simultaneously and at the same scale in the same neighborhoods.

Keywords ISAR; IPSVAR; IFDAR; community assembly; spatial ecology; taxonomic diversity, functional diversity; phylogenetic diversity.

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1 **Focusing on individual species reveals the specific nature of assembly mechanisms in**
2 **a tropical dry-forest.**

3

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14 **ABSTRACT**

15 We employed an individual-species approach based on the plant's eye perspective to
16 disentangle the effects of individual species on community assembly in a dry tropical forest of
17 southern Ecuador. We completely mapped a forest plot of 9 ha, and measured several
18 functional traits (leaf area, specific leaf area, wood density, seed mass and maximum height)
19 for tree and shrub species. To account for stochastic and habitat filtering effects, we fitted
20 spatial point processes for the 23 more abundant species in the plot, which confirmed that all
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28 evidences of facilitation (i.e., accumulated more TD than expected) but in some cases the
29 facilitated neighborhoods had more FD or PD than expected, suggesting the joint effect of
30 facilitation and competition based on niche differences. One species showed less TD than
31 expected, accompanied by lower FD and higher PD, suggesting competition based on fitness
32 differences.

33 Our study shows that in this dry tropical forest, where abiotic stress is prevalent, the
34 assembly of diversity is controlled by environmental heterogeneity and both facilitative and
35 competitive biotic processes, all of them acting simultaneously and at the same scale in the
36 same neighborhoods.

37 Keywords: ISAR, IPSVAR, IFDAR, community assembly, spatial ecology, taxonomic
38 diversity, functional diversity, phylogenetic diversity.

39 **Introduction**

40 One of the persistent questions in ecology is how biodiversity is maintained in
41 communities (Ricklefs, 1990). Modern coexistence theory assigns a prevalent role to niche-
42 based processes such as habitat filtering and competition (Chesson, 2000; HilleRisLambers
43 et al., 2012). As its name suggests, habitat filtering would select among the regional species
44 pool those species sharing traits best adapted to a particular (Weiher and Keddy 1999). On
45 the other hand, competition would impose a limiting similarity constraint (Abrams, 1983) if
46 trait differences are related to stabilizing niche differences (Chesson, 2000) or, alternatively, it
47 would promote the coexistence of species sharing similar traits related to competitive ability
48 (i.e., “fitness differences”; Mayfield and Levine, 2010). In studies addressing this questions,
49 species richness, i.e., taxonomic diversity (TD) has been the prevalent metric used to
50 characterize biodiversity from local to regional scales (Pavoine and Bonsall, 2011). During
51 the last decade, however, phylogenetic and functional information have been increasingly
52 used to test mechanistic community assembly hypotheses (Swenson, 2013) because
53 evidences indicate that functional traits and evolutionary history might also represent
54 independent aspects of community structure and dynamics (Pavoine and Bonsall, 2011;
55 Cadotte et al., 2013; Pavoine et al., 2012; Dainese et al., 2015). Functional diversity (FD) is
56 the variety of life-history traits present in any community (Mayfield et al., 2005). FD adds an
57 important dimension to the traditional characterization of taxonomic diversity, which, by
58 default, considers each species as ecologically equivalent (Faith, 2015). Phylogenetic
59 diversity (PD) summarizes the evolutionary past and the historical divergence among species
60 in a community (Faith, 1992), and has been also frequently employed as a proxy for
61 community assembly mechanisms (Gerhold et al., 2015). Incorporating FD and PD gives new
62 perspectives on the assembly processes with new insights about the abiotic and biotic
63 mechanisms driving communities (Helmus et al., 2007).

64 Although this methodological integration has fueled a boom of papers dealing with
65 different functional and phylogenetic aspects of community assembly (Pavoine and Bonsall,
66 2011), most of them are based on functional and phylogenetic summaries (e.g., weighted
67 means) of the community and, in consequence, disregard an important issue: the role of
68 individual species in structuring diversity. In fact, species interactions and inter-specific
69 fitness differences are at the core of most hypotheses and theories about community
70 assembly (Cheson, 2000; HilleRisLambers et al., 2012), so it is natural to ask about the role
71 played by each individual species, e.g., do certain species affect the structure of a
72 community? (Wiegand et al. 2007). Focusing on individual species, i.e. using the plant's eye
73 perspective (*sensu* Murrell et al., 2001), allows scrutinizing in detail the effects of ecological
74 processes on community assembly and might allow researchers to address questions such
75 as: do all species respond similarly to the assembly mechanisms generating neighborhoods
76 with foreseeable functional and/or phylogenetic structures? or, more specifically, are they
77 aggregating or repelling species with concrete functional and/or phylogenetic patterns, and,
78 are these responses consistent throughout space and time (e.g., along ontogeny; see
79 Espinosa et al., 2015)?

80 In this paper we investigate the processes ruling community assembly in a Neotropical
81 seasonal dry forest. This highly diverse and vulnerable ecosystem it is seasonally subjected
82 to a strong abiotic stress (Linares-Palomino et al., 2010), which suggests that functional
83 patterns (responses to current ecological processes) and morpho-functional adaptations
84 (resulting from evolutionary history) are necessarily involved in community assembly. It has
85 been suggested that in this type of forest, facilitative interactions prevail under unfavorable
86 environmental conditions (e.g. Espinosa et al., 2011; 2014). Using the plant's-eye perspective
87 (Murrell et al., 2001), we focus on individual species and analyze the effect of each one on
88 the structure of community diversity. We hypothesize that if facilitative interactions prevail,

89 most or at least some key (i.e., nurse), species would experience higher taxonomic diversity
90 in their close neighborhoods, whereas functional or phylogenetic diversity would not show
91 any particular pattern. On the contrary, if other mechanisms such as competition based on
92 niche differences or competition based on competitive ability differences are ruling
93 community assembly, we expect FD (and PD) increasing or decreasing respectively in those
94 neighborhoods (Table 1).

95 To test our hypothesis, we employ the Individual Species Area Relationship (ISAR;
96 Wiegand et al., 2007). Analogously to the proverbial Species-Area Relationship (Scheiner,
97 2003), the ISAR leads to estimate how species richness (i.e., TD) is spatially arranged
98 around the individuals of a particular species. Using fully mapped communities and
99 appropriate null models to control for the effects of environmental heterogeneity, the function
100 ISAR(r) allows assessing the effects of particular species on, and their responses to, local TD
101 at different spatial scales (i.e., at different radii r defining the neighborhoods; Wiegand et al.,
102 2007). To assess the structure of FD and PD in the same plant neighborhoods, we use two
103 analogous functions, i.e., the IFDAR(r) (Individual Functional Diversity–Area Relationship)
104 and the IPSVAR(r) (Individual Phylogenetic Species Variability -Area Relationship).
105 Contrasting ISAR, IFDAR and IPSVAR observations against the expectations of appropriate
106 null models allows distinguishing ‘accumulators’ and ‘repellers’ of TD, FD and PD, i.e.,
107 species whose individuals are surrounded by higher and lower diversity than expected at a
108 particular spatial scale, respectively (Wiegand et al., 2007). Both accumulation and repulsion
109 of TD, FD and PD have been interpreted as evidences for non-neutral or niche-based
110 processes that influence the distribution and diversity of tree species in forest communities
111 (Wiegand et al., 2007; Espinosa et al., 2015; Wang et al., 2016) and shrublands (Chacón-
112 Labella et al., 2016). If diversity around the individuals of a target species does not deviate
113 significantly from that expected, this is taken as evidence for neutrality (Wiegand et al., 2007;

114 Espinosa et al., 2015). The prevalence of these plant types within a community (i.e.,
115 accumulator, repeller and neutral) and the spatial scales at which such effects occur could
116 shed light on the biotic mechanisms implied in community assembly in mega-diverse
117 communities (Table 1).

118 As the influence of environmental heterogeneity and dispersal limitation in the distribution
119 of trees in this forest has been previously demonstrated (Jara-Guerrero et al., 2015), we test
120 the observed ISAR, IFDAR and IPSVAR functions against the expectations of individual null
121 models accounting for habitat filtering and stochastic processes. The joint use of the three
122 functions, then, would allow assigning patterns to specific interactive mechanisms (Table 1).
123 Thus, accumulator behavior in the ISAR function with neutral behavior for IPSVAR and
124 IFDAR would indicate pure facilitation (e.g., as in a stressful environmental context where
125 one or several "nurse species" expand habitat conditions in their neighborhood for other less
126 tolerant species). However, if the accumulator behavior of ISAR is accompanied with
127 accumulator behavior in IFDAR and/or IPSVAR, we could assume that the facilitator effect is
128 combined with a limiting similarity mechanism (i.e., with competition based on niche-
129 differences). On the contrary, an accumulator species for ISAR which shows a repeller
130 behavior for IFDAR and/or IPSVAR, indicates that its facilitative effect is accompanied by
131 some competitive processes based on fitness differences (Mayfield and Levine, 2010)
132 affecting the facilitated species (Table 1).

133 A repeller behavior for ISAR could be the consequence of competitive interactions with the
134 focal species (i.e. only some species are able to occur in the vicinity of the target species) or
135 among species facilitated by the focal species. If either IFDAR or IPSVAR functions (or both)
136 show neutral behavior, the mechanism that could determine the taxonomic exclusion would
137 probably be interference competition (Amarasekare, 2002) (Table 1). However, if combined
138 with accumulator values for IFDAR or IPSVAR the competition would be mediated by limiting

139 similarity. On the contrary, if IFDAR or IPSVAR show also repeller behaviors, that would
140 indicate that only certain competitive functional patterns could thrive under the canopy or in
141 the close vicinity; thus we could assume that competition among the focal species and its
142 neighbors or among the facilitated neighbors is mediated by fitness differences. Of course,
143 these combinations could vary depending on the existence (or not) and the prevalence of
144 phylogenetic niche conservatism and possible evolutive convergence affecting the traits
145 involved in the coexistence of individual species (Chacón-Labela et al., 2016).

146

147 MATERIAL AND METHODS

148 Study site

149 The study was conducted in the tropical dry forest of Arenillas Ecological Reserve (REA,
150 from its Spanish acronym), located in the southwestern most tip of Ecuador (03°34'15.44"S;
151 80°08'46.15"E, 30 m a.s.l.) in El Oro province, between the towns of Arenillas and Huaquillas.
152 This Reserve covers 131.7 km² with an altitude ranging from 0 to 300 m. This area is
153 occupied by a transitional formation between dry deciduous forests and dry scrubs of
154 lowlands. The most conspicuous tree species in the area are *Tabebuia billbergii* (Bureau & K.
155 Schum.) Standl, *T. chrysantha* (Jacq.) G. Nicholson (Bignoniaceae) and *Ceiba trichistandra*
156 (A. Gray) Bakh. (Bombacaceae), other species like *Croton* spp. (Euphorbiaceae) and
157 *Colicodendron scabridum* (Kunth) Seem. (Capparaceae), become more important in the dry
158 scrub formation. These tropical dry forests are considered the most threatened ecosystems in
159 Ecuador (Gentry, 1977; Sierra, 1999; Espinosa et al., 2015).

160

161 The climate is characterized by a rainy season with an average annual rainfall of 515 mm
162 from January to April (wet season) and only 152 mm on average during the eight-month dry
163 season (weather station Huaquillas for the period 1969–2014). The average temperature is

164 25.2°C with a maximum variation of 3.4 °C **between** the coldest and warmest month. The
165 lower temperatures occur during the dry season.

166 **In the center of the REA, a square, 300 x 300 m (i.e., 9 hectares) permanent plot (i) was**
167 **installed in 2009, and all trees and shrubs) with DBH ≥5cm were tagged and identified at the**
168 **species level. Average density (+-s.e.) of trees and shrubs in this area is (409 ± 17 trees/ha**
169 **and 183 ± 48 shrubs / ha.** During the dry season (July to September 2010 and 2011) tagged
170 plants were mapped using a total station, Leica TS02-5 Power. The average canopy height of
171 the forest in the plot is 15 m (Espinosa et al., 2016). The topography in the plot is quite flat,
172 with some small depressions. **Soil is mostly sandy loam.** For the analysis of the effect of
173 individual species on community diversity, we selected the 23 species (15 trees, 8 shrubs)
174 with had more than 16 individuals (Table S1 in Supporting Information).

175

176 **Functional trait collection**

177 All the traits were measured following standardized protocols (Cornelissen et al., 2003;
178 Pérez-Harguindeguy et al., 2013). We measured functional traits for all trees and shrubs in
179 the permanent plot. For each species, we randomly collected 10 sun leaves from each of 50
180 individuals, i.e., a total of 500 leaves by species. Leaves were collected during the phenologic
181 peak. Leaf area (LS) was measured with the program Image J (Abràmoff et al., 2004; Kraft
182 and Ackerty, 2010). Specific leaf area (SLA) was calculated as the fresh leaf area divided by
183 the leaf dry mass (after 48 hours drying at 80 °C). For species with compound leaves, the
184 rachis was included in the measurements.

185 To estimate wood density (WD), we collected five secondary branches (with a circumference
186 between 10-20 cm) for three individuals per species. Fresh wood volume was determined
187 with the water displacement method (Chave, 2006), after which samples were oven-dried at

188 80°C and weighed. When this was not feasible, we employed the Global wood density
189 database of Chave et al. (2009) and Zanne et al. (2009). In this case, if there were several
190 density measurements for a species, we calculated and used their mean. Maximum height
191 (H_{\max}) was measured by using a compact Electronic Laser Hypsometer TruPulse 360°, from
192 the base to the uppermost tip of trees.

193 Seeds were collected from at least 10 fruits taken from different individuals of each species.
194 Seed mass (SM) was obtained after 48 hours drying at 80 °C. For ten species, which could
195 not be collected in the field, SM was approximated by the average SM of congeneric species
196 recorded in the database of Royal Botanic Gardens Kew (Royal Botanic Gardens Kew,
197 2014).

198 **Phylogeny construction**

199 A phylogenetic tree for the sampled species was built (Figure S1 in Supporting
200 Information), by using the program Phylomatic and the megatree version R20120829 (Webb
201 and Donoghue, 2005; available online). Branch lengths were estimated for each tree using
202 the BLADJ algorithm implemented in Phylocom (Webb et al., 2008), based on the ages of
203 fossils of plants reported by Wikström et al., (2001). The "ape" package (Paradis, 2004)
204 library was used to import and manipulate the phylogeny in R (R Development Core Team,
205 2014).

206 **Spatial pattern analyses**

207 For each of the 23 target species, we first selected a spatial point process, compatible with its
208 realized spatial pattern, to be used as a null model. In order to find the appropriate null model
209 for each species, we followed an approach conceptually similar to the pattern reconstruction
210 strategy of Wiegand et al. (2013), as implemented by Pescador et al. (2014) and Jara-
211 Guerrero et al. (2015). To begin with, we fitted a battery of different spatial null models for

212 each species: (1) a homogeneous Poisson process (HPP) with constant intensity λ equal to
213 the density of the observed pattern in the map; (2) a homogeneous Poisson cluster process
214 (HPCP) with constant intensity λ and parameters σ and ρ fitted by minimum contrast (Diggle,
215 2003); (3) inhomogeneous Poisson processes (IPP) with an intensity function $\lambda(x, y)$
216 estimated with a Gaussian kernel (Wiegand et al., 2007) with 13 different σ values
217 (bandwidths), from $\sigma = 15$ to $\sigma = 75$ m in 5 m intervals; and, finally, (4) inhomogeneous
218 Poisson cluster processes (IPCP) (Waagepetersen, 2007) with bandwidth-values similar to
219 those considered for the IPPs. Then, to select the null model that best describes the spatial
220 properties of each species, we computed the homogeneous (or inhomogeneous) K-function
221 for the observed spatial pattern of the species and compared it to the average of the K
222 functions of 199 simulations for each null model. The best model for each species was
223 selected with the goodness-of-fit u statistic (Diggle, 2003; Loosmore and Ford, 2006;
224 Pescador et al., 2014). K functions were computed from $r=0$ to $r=60$ m, with 1 m increments.

225 It is important to remind that by doing this main determinants of the individual spatial
226 pattern of each species, including the effects of environmental heterogeneity (i.e., habitat
227 filtering), are taken into consideration.

228

229 **Individual diversity-area relationships**

230 For each species we summarized the structure of the three community diversity
231 components around the individuals of each species: TD using the ISAR function, FD with the
232 IFDAR-function, and PD with the IPSVAR-function (De la Cruz, 2017). The $ISAR_t(r)$ function
233 (Wiegand et al., 2007) estimates the expected number of species within circular areas with
234 radius r around an average individual of a target species t . To calculate $ISAR_t(r)$, we first
235 calculated the bivariate emptiness probability $P_{tj}(0, r)$ that species j was not present in circles
236 with radius r around plants of the target species t (without counting the focal stem if $t = j$) and

237 we then summed $1 - P_{ij}(0, r)$ for all species (N) present in the plot. ISAR was then estimated
 238 for each species t as follows:

$$239 \quad ISAR_t(r) = \sum_{j=1}^N [1 - P_{tj}(0, r)]$$

240 The Individual Functional Diversity-Area Relationship $IFDAR_t(r)$ is the expected FD within
 241 circular areas with radius r around a typical individual of a focal species t . It is estimated as:

$$242 \quad IFDAR_t(r) = \frac{\sum_{i=1}^n FDis_i(r)}{n}$$

243 where n is the total number of individuals of the focal species and $FDis_i(r)$ is the functional
 244 dispersion (Laliberté and Legendre, 2010) of the "local" community delimited by the circle
 245 within with radius r around an individual i of the focal species. For a community, $FDis$ is
 246 computed as:

$$247 \quad FDis = \frac{\sum_{j=1}^S x_j z_j}{\sum_{j=1}^S x_j}$$

248 where S is the total number of species, x_j is the abundance of species j in the community
 249 and z_j is the distance (usually Gower's distance) in the multivariate space of traits from
 250 species j to the centroid of the community (Laliberté and Legendre, 2010). In the same way,
 251 we estimated $IPSVAR_t(r)$, the expected phylogenetic species variability within circular areas
 252 with radius r around an average individual of the target species t as:

$$253 \quad IPSVAR_t(r) = \frac{1}{n} \sum_{i=1}^n PSV_i(r)$$

254 were $PSV_i(r)$ is the Phylogenetic Species Variability index (Helmus et al., 2007) computed
255 for communities within circles of radius r around each i of n individuals of the target species.
256 PSV quantifies how phylogenetic relatedness decreases the variance of a hypothetical
257 unselected/neutral trait shared by all species in a community, so it is directly related to mean
258 phylogenetic distance. Its expected value is 1 when all species in a sample are unrelated
259 (i.e., a star phylogeny) and approaches zero as species become more related. It is computed
260 as $1 - \bar{c}$, where \bar{c} is the average of the off-diagonal elements of the covariance matrix that
261 summarizes the correlation structure of the community phylogeny (Helmus et al., 2007).
262 To avoid difficulties due to small sample size we only calculated functions for species with at
263 least 16 individuals in the plot. All the individual species-area functions were computed from
264 $r=1$ to $r=60$ m, with 1 m increments.

265 We inferred the significance of the deviations of the observed *ISAR*, *IFDAR* and *IPSVAR*
266 functions comparing them with simulation envelopes based on 199 simulations of the best
267 model fitted in the previous step.

268 Deviations from the null model predictions were assessed with the Studentized maximum
269 absolute difference (MAD) envelope test of Myllymäki et al. (2017) for three spatial scales,
270 i.e., for three ranges of neighborhood radii: from 1 to 20 m, 21 to 40 m and 41 to 60 m.
271 Species that showed significant positive or negative deviations from the null model in any of
272 these ranges were considered respectively as accumulators or repellers of diversity at such
273 spatial scales. Species that did not show deviations from the null model at any of the three
274 spatial ranges were considered as "neutrals". It is important to take into consideration that our
275 null model approach eliminates the spatial signal due to the environmental heterogeneity at
276 the corresponding scales leaving alone the effect of plant-to-plant interactions (Chase and
277 Myers, 2011). All calculations were done using the R statistical software, version 3.1.0 (R
278 Development Core Team, 2014). Null models were fitted using the packages spatstat

279 (Baddeley et al., 2015) and selectspm (Jara-Guerrero et al., 2015). The ISAR, IFDAR and
280 IPSVAR analyses were implemented using the package “idar” (De la Cruz, 2017), and the
281 Studentized MAD envelope test using the package “sppptest” (Myllymäki et al., 2017).

282 RESULTS

283 As expected for an ecosystem where high abiotic stress is prevalent, the analyses
284 showed the importance of environmental heterogeneity in the distribution of trees and shrubs
285 in this forest. All the studied species were best described by inhomogeneous point
286 processes, with inhomogeneous Poisson cluster (IPCP) and inhomogeneous Poisson (IPP)
287 processes best fitting the spatial pattern of fourteen and nine species respectively (Table S2
288 in Supporting Information).

289 For any particular value of r between 1–60 m, the most prevalent behavior for the 23
290 tested species was neutral for ISAR (52 %, 12 species), IFDAR (57%, 13 species) and
291 IPSVAR (70 %, 16 species) (Figure 1). With respect to ISAR, 13 species showed an
292 accumulator behavior at the fine spatial scale (i.e., 1-20 m), and eight of them extended this
293 behavior along the whole range studied (1-60 m). Only one species, *Chloroleucon*
294 *mangense*, behaved as repeller and showed this behavior in the whole range of distances (1-
295 60 m) (Table 2; Figure 2).

296

297 In relation to IFDAR, only 4 species were accumulators at fine scale, with one species
298 (*Jacquinia sprucei*) extending this behavior along the whole range. *Achatocarpus pubescens*
299 was neutral at fine scale but accumulator at medium and large scales. Only one species,
300 *Armatoceurus cartwrightianus*, behaved as repeller at fine scale (and extended this behavior
301 to the full range of scales); *Chloroleucon mangense* was neutral at fine scales and behaved
302 as repeller at medium and large scales (Table 2; Figure 2).

303 Finally, in the case of IPSVAR, four species showed accumulator behavior at fine scale
304 (1-20 m). One of them, *Chloroleucon mangense*, was accumulator also in the medium range
305 (21-40 m). Other species, such as *Armatocereus cartwrightianus* and *Cynophalla mollis*,
306 showed accumulator behavior at medium and large scales, respectively, and behaved as
307 neutral in the rest of the spatial range. *Jacquinia sprucei* was repeller at fine and medium
308 scales and accumulator at the largest range (Table 2).

309 Considering all the diversity components together, we found that only eight species were
310 completely neutral for the three Individual Diversity-Area summary functions. On the contrary,
311 only one species (*Jacquinia sprucei*) deviated from the expectations of the null model at all
312 scales, behaving as an accumulator for TD and FD but as repeller for PD. The rest of the
313 species showed different combinations of results for each diversity. Focusing on the fine
314 scales, the second more common pattern after the completely neutral one (8 species) was
315 accumulator for ISAR and neutral for both IFDAR and IPSVAR (5 species). Other four
316 species were accumulator for ISAR and accumulator for either IFDAR or IPSVAR (or both).

317

318 **DISCUSSION**

319 The current scientific consensus suggests that the composition and local structure of a
320 plant community is the result of stochastic and deterministic processes (HilleRisLambers et
321 al., 2012), sometimes called "community assembly processes" (Götzenberger et al., 2012),
322 acting together. Our results, based on an individualistic species approach, show clear
323 evidences of several of these processes, including dispersal limitation, habitat filtering and
324 plant-to-plant interactions (i.e. facilitation and competition) ruling community assembly in the
325 southern Ecuadorian dry tropical forest of the REA. Confirming the findings of Jara-Guerrero
326 et al. (2015) we found that 14 out of the 23 studied species were best described by IPCP

327 processes, i.e., spatial processes including dispersal limitation. This is not surprising as the
328 prevalence of dispersal limitation in tropical forests it is a well-known fact (i.e., Condit et al.,
329 2000). All the best-fit spatial processes selected for the target species were also
330 inhomogeneous, which suggest the relevance of environmental heterogeneity (i.e., habitat
331 filtering) for community assembly. This result is especially relevant because it shows that the
332 effects of environmental heterogeneity vary within the relative small scale of the plot (9 ha), in
333 contrast with the extended view, within the general framework of modern coexistence theory,
334 that the habitat filters the regional species pool at coarser scales (Cornwell and Ackerly,
335 2009.), i.e., at scales coarser than those where the effects of species interactions take place.
336 Although the effects of environmental heterogeneity at finer scales is a well-known fact within
337 the ecological point pattern literature (e.g., Wiegand and Moloney, 2014), only recently this
338 idea is permeating other ecological fields (Chase, 2014).

339 Since dry forests occur in harsh environments dominated by water shortages and
340 pronounced seasonality in precipitation, it is frequently assumed that facilitative interactions
341 would be the norm and influence community structure and composition (Espinosa et al.,
342 2013, 2015). Our main hypothesis was that facilitative processes would be prevalent among
343 species interactions in the REA dry forest. In agreement with this prediction, we found that a
344 large number of species (11 out of 23) showed accumulative behavior for ISAR (i.e., more TD
345 than expected) at fine scales (1-20 m). This is the spatial range where the direct effects of
346 interactions among individual plants could be expected and detected (Hubbell et al., 2001;
347 Uriarte et al., 2004). The accumulation of TD at short spatial scales in **environments where**
348 **abiotic stress is prevalent** it has been interpreted as a consequence of the effect of some
349 individual species (i.e. nurse species) expanding the habitat requirements of other species in
350 their neighborhood (Chacón-Labela et al., 2014; Espinosa et al., 2015). In the REA,
351 however, this interpretation should be reconsidered cautiously on a per-species basis since

352 some of the accumulators of TD in our study are also fine-scale accumulators of FD or PD
353 (see Table 2). The increase of FD in a community, with values larger than expected for a null
354 model of community assembly, is usually considered evidence of the effect and prevalence of
355 competition (i.e., limiting similarity; Cornwell and Ackerly, 2006; Kraft and Ackerly, 2010). It
356 seems, therefore, that the enhancement of environmental conditions, which allows an
357 increase of TD in these cases, goes together with the establishment of strong competitive
358 processes within the ameliorated microhabitats. This joint effect of facilitation and limiting
359 similarity within enhanced patchy habitats has been reported in other ecosystems, such as
360 dry alkali grasslands (Kelemen et al., 2015), where trait diversity among the facilitated
361 species was found to increase with the biomass of the nurse species. In the REA, this effect is
362 mediated by both trees (*Jacquinia sprucei*, *Tabebuia billbergii*) as well as by shrubs
363 (*Achatocarpus pubescens*, *Malphigia emarginata*) so the biomass explanation does not apply
364 here. On the other hand, there are also trees and shrubs among the eight neutral species, so
365 plant life form does not seem to be implied in these mechanisms.

366 In the REA we found two facilitator species (*Achatocarpus pubescens* and *Tabebuia*
367 *billbergii*), which, in addition to TD, increased PD in their neighborhoods. Some authors (e.g.,
368 Valiente-Banuet and Verdú, 2007) have explained that facilitation can increase the
369 phylogenetic diversity of communities by securing the regeneration niche of species distantly
370 related to their facilitators, which otherwise would have been filtered out by the harsh
371 environmental conditions. This does not seem to be the case in our forest; where there are
372 not species unambiguously associated to both facilitators, so the local increase in
373 phylogenetic diversity could be also a consequence of competitive processes (Webb et al.,
374 2002).

375 Only one species showed repeller behavior for TD at fine scales, i.e., *Chloroleucon*
376 *mangense*. Previous studies about the effects of individual species on TD have interpreted

377 the existence of repeller species as the result of competitive processes (e.g., a focal repeller
378 species interfering the establishment of other species and resulting in species poor
379 neighborhoods; Wiegand et al., 2007). If it were a genuine case of interference competition
380 (Amarasekare, 2002) no significant pattern for FD would be found. However, *Chloroleucon*
381 *mangense* is also a FD repeller, which suggests that the low TD in the neighborhoods around
382 its individuals is a consequence of competition based on fitness differences (Chesson 2000,
383 Mayfield and Levine, 2010). Curiously, *C. mangense* is also an accumulator of PD at fine
384 scales. If differences in competitive ability are responsible for these patterns of TD and FD, it
385 would mean that the trait(s) mediating this process are phylogenetically dispersed (i.e.,
386 character displacement, Dayan and Simberloff, 2005). This could be the consequence of a
387 limited number of clades evolving in response to strong competitive processes (where the
388 studied functional traits were involved) in the relatively isolated (from a biogeographical point
389 of view) Tumbesian forests (Dayan and Simberloff, 2005; Ackerly, 2009). All considered traits
390 show less phylogenetic signal than expected under Brownian evolution (Bloomberg's K
391 between 0.43 and 0.57), which supports our interpretation, but given the low power provided
392 by our small phylogeny, only for wood density the result is statistically significant. This finding
393 however does not deny the possibility that other functional traits not considered in this study
394 could have remained conserved in the phylogeny and that the responses that we are
395 revealing could arise from some environmental filtering effect on these traits. Nevertheless,
396 this is improbable due to the well-known phenotypic integration of most plant functional traits
397 (Pigliucci 2003).

398 Almost a third of the studied focal species (8 species) showed neutral behavior for TD,
399 FD and SD at fine scales. Although a first interpretation could try to explain this results as a
400 consequence of species depending only on stochastic mechanisms and habitat filtering
401 (which we accounted for with the null models), recent theoretical developments predict that in

402 species-rich communities, stochastic dilution effects, i.e., pure geometrical mechanisms
403 caused by the high number of species, would blur non-random patterns generated by
404 competitive or facilitative interactions (Wang et al., 2016).

405 In conclusion, our individual species approach, with the joint consideration of the
406 individual species responses to and effects on the three complementary pillars of diversity
407 (TD, FD and PD) within a framework of point pattern processes provides insights on the role
408 of plant-to-plant interactions and other mechanisms in the assembly of this seasonal tropical
409 dry forest. The main contribution of our approach is that it easily allows disentangling the role
410 played by each species in community assembly.

411 Our framework, which is based on the use of null models reproducing processes of
412 sound ecological sense, can be easily extended to other diversity metrics than can help to
413 shed light on coexistence process by considering the individual species perspective
414 simultaneously at many spatial scales. For instance, in our Neotropical dry forest the
415 apparent dominance of neutral processes and facilitation after surveying only TD (Espinosa
416 et al., 2015) turned to non-neutral prevalence when the other diversity components are
417 evaluated simultaneously.

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424 **ACKNOWLEDGMENTS**

425 We thank to Gusmán A, Gusmán J, Benítez A. for their assistance in fieldwork and to Ramón
426 P for his assistance in the statistical analysis. We thank David Duncan for English language
427 revision. Alicia Ledo, the editor and one anonymous reviewer provided valuable comments
428 that improved a previous version of the manuscript.

429 This work has been partially supported by projects A/024796/09 and A/030244/10 financed
430 by Agencia Española de Cooperación Internacional y para el Desarrollo (AECID-2010-2011),
431 projects Islas-Espacio CGL2009-13190-C03-02; ROOTS [CGL2015-66809-P] financed by
432 the Spanish Ministerio de Economía, project REMEDINAL3 [S2013/MAE-2719] financed by
433 Comunidad de Madrid; the project PROY_CCNN_0030 and 0054 Universidad Técnica
434 Particular de Loja (UTPL); Secretaria de Educación Superior, Ciencia, Tecnología e
435 Innovación (SENESCYT - <http://www.educacionsuperior.gob.ec/>) scholarship program 2009
436 and International Tropical Timber Organization (ITTO-
437 http://www.itto.int/es/fellowship_detail/id=3805) scholarship program 2013.

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642 **FIGURES**

643 Figure1: Proportion of significant accumulator, repeller and neutral species for ISAR
644 (Individual Species-Area Relationships), IFDAR (Individual Functional-Diversity–Area
645 Relationship) and IPDAR (Individual Phylogenetic -Area Relationship) in the REA, when
646 considering different spatial scales (i.e., circular neighborhoods with radii 1-60 m).

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648 Figure 2. Test of the individual diversity-area functions against the null model for *Chlorella*
649 *mangense* (a) ISAR (Individual Species–Area Relationship) (b) IFDAR (Individual functional-
650 diversity–area relationship). The black line represent the observed function and the grey
651 areas correspond to the envelopes computed from 199 simulations of *Chlorella*
652 *mangense* patterns from the null model. The red dashed line represents the expectations
653 from the null model.

654 **Supporting Information**655 **Table S1. The 23 species (15 trees, 8 shrubs) with more than 16 individuals, belonging**
656 **to 16 families for analysis.**
657

Familia	Genero	Especies	Form habitat
ACHATOCARPACEAE	<i>Achatocarpus</i>	<i>Achatocarpus pubescens</i> C.H. Wright	shrub
CACTACEAE	<i>Armatocereus</i>	<i>Armatocereus cartwrightianus</i> (Britton & Rose) Backeb. ex AW Hill	shrub
BURSERACEAE	<i>Bursera</i>	<i>Bursera graveolens</i> (Kunth) Triana & Planch.	tree
FABACEAE	<i>Caesalpinia</i>	<i>Caesalpinia glabrata</i> Kunth	tree
FABACEAE	<i>Chloroleucon</i>	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	tree
POLYGONACEAE	<i>Coccoloba</i>	<i>Coccoloba ruiziana</i> Lindau	shrub
BIXACEAE	<i>Cochlospermum</i>	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	tree
CAPPARACEAE	<i>Colicodendron</i>	<i>Colicodendron scabridum</i> (Kunth) Seem.	tree
BORAGINACEAE	<i>Cordia</i>	<i>Cordia lutea</i> Lam.	shrub
EUPHORBIACEAE	<i>Croton</i>	<i>Croton rivinifolius</i> Kunth	shrub
CAPPARACEAE	<i>Cynophalla</i>	<i>Cynophalla mollis</i> (Kunth) J. Presl	tree
MALVACEAE	<i>Eriotheca</i>	<i>Eriotheca ruizii</i> (K. Schum.) A. Robyns	tree
FABACEAE	<i>Erythrina</i>	<i>Erythrina velutina</i> Willd.	tree
ERYTHROXYLACEAE	<i>Erythroxyllum</i>	<i>Erythroxyllum glaucum</i> O.E. Schulz	tree
FABACEAE	<i>Geoffroea</i>	<i>Geoffroea spinosa</i> Jacq.	tree

PRIMULACEAE	<i>Jacquinia</i>	<i>Jacquinia sprucei</i> Mez	tree
LEGUMINOSAE	<i>Leucaena</i>	<i>Leucaena trichodes</i> (Jacq.) Benth.	shrub
MALPIGHIACEAE	<i>Malpighia</i>	<i>Malpighia emarginata</i> DC.	shrub
FABACEAE	<i>Piptadenia</i>	<i>Piptadenia flava</i> (DC.) Benth.	shrub
NYCTAGINACEAE	<i>Pisonia</i>	<i>Pisonia aculeata</i> L.	tree
LEGUMINOSAE	<i>Pithecellobium</i>	<i>Pithecellobium excelsum</i> (Kunth) Mart.	tree
BIGNONIACEAE	<i>Tabebuia</i>	<i>Tabebuia billbergii</i> (Bureau & K. Schum.) Standl.	tree
BIGNONIACEAE	<i>Tabebuia</i>	<i>Tabebuia chrysantha</i> (Jacq.) G. Nicholson	tree

659 **Table S2.** Models selected for each species on the basis of a goodness-of-fit-test (*p*
660 values). IPCP: inhomogeneous Poisson cluster process; IPP: inhomogeneous
661 Poisson process

Species	Best model	<i>p</i>-value
1. <i>Armatocereus cartwrightianus</i>	IPCP	0.53
2. <i>Bursera graveolens</i>	IPCP	0.9
3. <i>Caesalpinia glabrata</i>	IPCP	0.61
4. <i>Coccoloba ruiziana</i>	IPCP	0.64
5. <i>Colicodendron scabridum</i>	IPCP	0.88
6. <i>Cordia lutea</i>	IPCP	0.61
7. <i>Croton rivinifolius</i>	IPCP	0.8
8. <i>Erythrina velutina</i>	IPCP	0.64
9. <i>Erythroxylum glaucum</i>	IPCP	0.68
10. <i>Geoffroea spinosa</i>	IPCP	0.67
11. <i>Leucaena trichodes</i>	IPCP	0.82
12. <i>Malpighia emarginata</i>	IPCP	0.86
13. <i>Piptadenia flava</i>	IPCP	0.77
14. <i>Tabebuia chrysantha</i>	IPCP	0.70
15. <i>Achatocarpus pubescens</i>	IPP	0.83
16. <i>Chloroleucon mangense</i>	IPP	0.62

17. <i>Cochlospermum vitifolium</i>	IPP	0.93
18. <i>Cynophalla mollis</i>	IPP	0.82
19. <i>Eriotheca ruizii</i>	IPP	0.77
20. <i>Jacquinia sprucei</i>	IPP	0.67
21. <i>Pisonia aculeata</i>	IPP	0.90
22. <i>Pithecellobium excelsum</i>	IPP	0.93
23. <i>Tabebuia billbergii</i>	IPP	0.79

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664 **Figure S1.** Phylogenetic tree including the 48 plant species recorded in the 9 hectares
665 permanent plot in REA. Red line represents 100 m.y

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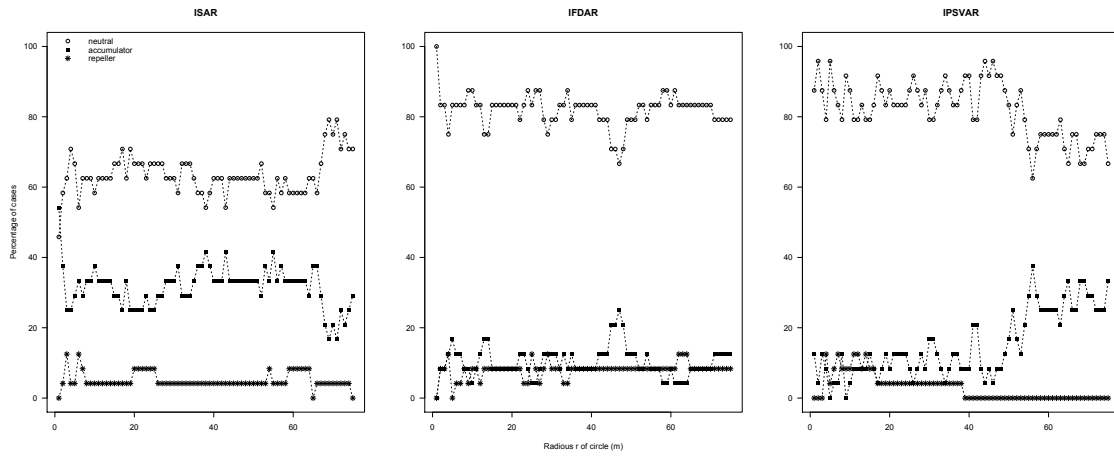
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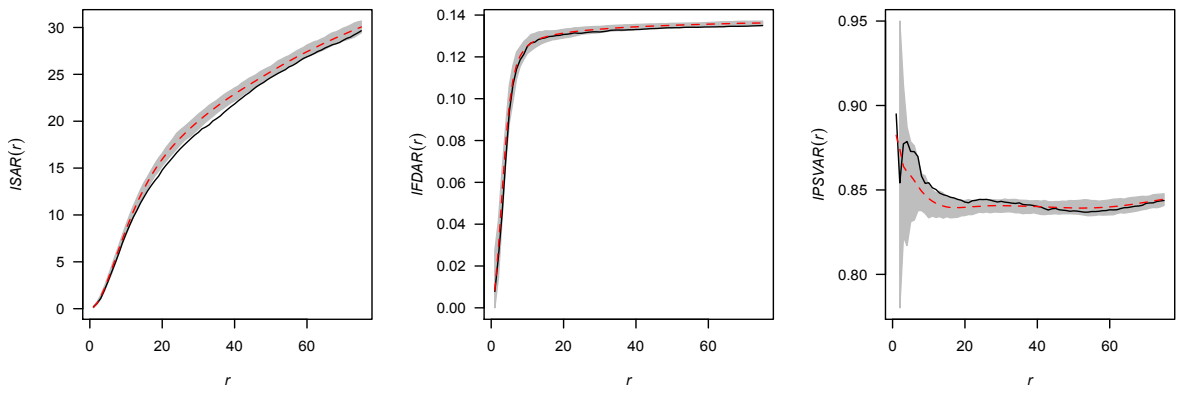
1 Figure1.



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4 Figure 2.



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1 **Tables**

2 **Table1:** Interpretation of the **biotic** processes implied in the assembly of plant communities
 3 as an output of the behavior in relation with three spatial diversity functions.

ISAR	IFDAR	IPSVAR	INTERPRETATION
Accumulator	Neutral	Neutral	Taxonomic enrichment. Facilitation by a nurse independently of the phylogenetic relationship with and/or the functional traits of the facilitated species
Accumulator	Accumulator	Accumulator/Repeller	Facilitation and limiting similarity. The nurse species generates microhabitats where competition based on niche differences promotes niche partitioning, increases functional diversity and, depending on the conservation or divergence of traits along the phylogeny, increases or decreases phylogenetic diversity.
Accumulator	Repeller	Accumulator/Repeller	Facilitation and competition based on fitness differences. The nurse species generates microhabitats where only species with the highest competitive ability could enter. This decreases functional diversity and, depending on the conservation or divergence of traits along the phylogeny, increases or decreases phylogenetic diversity.
Repeller	Neutral	Neutral	Interference competition. A competitive species interferes with any other species independently of their phylogenetic and/or functional similarity.
Repeller	Accumulator	Accumulator/Repeller	Competition mediated by limiting similarity. Competition between the focal species and its neighbors favors niche partitioning and promotes higher FD. Depending on the conservation or dispersion of the related traits along the phylogeny, it increases or

			decreases PD.
Repeller	Repeller	Accumulator/Repeller	<p>Competition based on fitness differences. Competition between the focal species and its neighbors or competition induced under the favorable conditions generated by the focal species favors species with the highest competitive ability and therefore decreases FD. Depending on the conservation or dispersion of the related traits along the phylogeny, it increases or decreases PD.</p>
Neutral	Accumulator	Accumulator/Repeller	<p>Genuine limiting similarity without signal in the taxonomic diversity. Accumulator behavior of species in phylogenetic and/or functional diversity causes that similar phylogenetic and/or functional species cannot co-occur. However, this response does not affect the taxonomic diversity.</p>
Neutral	Repeller	Accumulator/Repeller	<p>Genuine competition based on fitness differences. Only species functionally similar, with the highest competitive ability, could coexist in the same neighborhood. However, this response does not affect the taxonomic diversity.</p>

5 **Table 2:** p-values of the Studentized Maximum Deviation Test for three spatial ranges: 1–20, 21–40 and 41–60 m. Shaded cells indicate
6 significant deviations from the null model (after accounting for the false discovery rate) and therefore accumulator or repeller behavior. Grey
7 background: species that behaved as accumulators in the evaluated range. Black background: species that behaved as repellers in the
8 evaluated range. Neutral behavior is showed as white cells. ISAR (Individual Species–Area Relationship), IFDAR (Individual Functional-
9 Diversity–Area Relationship) and IPSVAR (Individual Phylogenetic Species Variability -Area Relationship).
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Species	N	Growth form	ISAR			IFDAR			IPSVAR		
			R1-20	R21-40	R41-60	R1-20	R21-40	R41-60	R1-20	R21-40	R41-60
<i>Achatocarpus pubescens</i>	137	shrub	0.005	0.990	0.075	0.710	0.020	0.040	0.030	0.700	0.690
<i>Armatocereus cartwrightianus</i>	394	shrub	0.005	0.290	0.375	0.005	0.005	0.005	0.265	0.035	0.045
<i>Bursera graveolens</i>	114	tree	0.205	0.090	0.115	0.675	0.790	0.935	0.855	0.140	0.100
<i>Caesalpinia glabrata</i>	197	tree	0.005	0.010	0.025	0.465	0.395	0.475	0.635	0.515	0.095
<i>Chloroleucon mangense</i>	277	tree	0.005	0.005	0.005	0.265	0.020	0.005	0.040	0.035	0.320
<i>Coccoloba ruiziana</i>	130	shrub	0.105	0.340	0.080	0.540	0.780	0.225	0.060	0.755	0.530
<i>Cochlospermum vitifolium</i>	240	tree	0.210	0.065	0.145	0.875	0.395	0.665	0.355	0.145	0.100
<i>Colicodendron scabridum</i>	233	tree	0.275	0.105	0.130	0.235	0.770	0.405	0.040	1.000	0.495
<i>Cordia lutea</i>	16	shrub	0.030	0.465	0.265	0.615	0.500	0.115	0.580	0.610	0.480
<i>Croton rivinifolius</i>	813	shrub	0.165	0.635	0.925	0.190	0.445	0.390	0.195	0.515	0.325
<i>Cynophalla mollis</i>	595	tree	0.005	0.005	0.005	0.205	0.295	0.145	0.445	0.175	0.010
<i>Eriotheca ruizii</i>	286	tree	0.005	0.005	0.005	0.055	0.600	0.790	0.495	0.505	0.790
<i>Erythrina velutina</i>	41	tree	0.055	0.155	0.133	0.035	0.450	0.970	0.430	0.105	0.140
<i>Erythroxyllum glaucum</i>	293	tree	0.005	0.340	0.485	0.585	0.675	0.650	0.325	0.840	0.545
<i>Geoffroea spinosa</i>	272	tree	0.020	0.005	0.010	0.415	0.470	0.835	0.655	0.590	0.120
<i>Jacquinia sprucei</i>	52	tree	0.005	0.005	0.005	0.005	0.005	0.005	0.005	0.005	0.005
<i>Leucaena trichodes</i>	485	shrub	0.825	0.410	0.490	0.140	0.760	0.555	0.190	0.615	0.950
<i>Malpighia emarginata</i>	576	shrub	0.005	0.005	0.015	0.005	0.375	0.170	0.130	0.185	0.065
<i>Piptadenia flava</i>	167	shrub	0.360	0.265	0.415	0.130	0.075	0.595	0.105	0.585	0.775
<i>Pisonia aculeata</i>	18	tree	0.070	0.350	0.685	0.360	0.845	0.645	0.175	0.080	0.530
<i>Pithecellobium excelsum</i>	162	tree	0.010	0.030	0.030	0.610	0.110	0.070	0.375	0.070	0.105
<i>Tabebuia billbergii</i>	527	tree	0.005	0.145	0.110	0.005	0.050	0.590	0.030	0.700	0.690
<i>Tabebuia chrysantha</i>	388	tree	0.045	0.560	0.360	0.355	0.180	0.580	0.020	0.535	0.380

