



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

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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.

1. Introduction

One of the persistent questions in ecology is how biodiversity is maintained in communities (Ricklefs, 1990). Modern coexistence theory assigns a prevalent role to niche-based processes such as habitat filtering and competition (Chesson, 2000; HilleRisLambers et al., 2012). As its name suggests, habitat filtering would select among the regional species pool those species sharing traits best adapted to a particular (Weiher and Keddy, 1999). On the other hand, competition would impose a limiting similarity constraint (Abrams, 1983) if trait differences are related to stabilizing niche differences (Chesson, 2000) or, alternatively, it would promote the coexistence of species sharing similar traits related to competitive ability (i.e., “fitness differences”; Mayfield and Levine, 2010). In studies addressing this questions, species richness, i.e., taxonomic diversity (TD) has been the prevalent metric used to characterize biodiversity from local to regional scales

(Pavoine and Bonsall, 2011). During the last decade, however, phylogenetic and functional information have been increasingly used to test mechanistic community assembly hypotheses (Swenson, 2013) because evidences indicate that functional traits and evolutionary history might also represent independent aspects of community structure and dynamics (Pavoine and Bonsall, 2011; Cadotte et al., 2013; Pavoine and Ricotta, 2012; Dainese et al., 2015). Functional diversity (FD) is the variety of life-history traits present in any community (Mayfield et al., 2005). FD adds an important dimension to the traditional characterization of taxonomic diversity, which, by default, considers each species as ecologically equivalent (Faith, 2015). Phylogenetic diversity (PD) summarizes the evolutionary past and the historical divergence among species in a community (Faith, 1992), and has been also frequently employed as a proxy for community assembly mechanisms (Gerhold et al., 2015). Incorporating FD and PD gives new perspectives on the assembly processes with new insights about the abiotic and biotic

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mechanisms driving communities (Helmus et al., 2007).

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

In this paper we investigate the processes ruling community assembly in a Neotropical seasonal dry forest. This highly diverse and vulnerable ecosystem it is seasonally subjected to a strong abiotic stress (Linares-Palomino et al., 2010), which suggests that functional patterns (responses to current ecological processes) and morpho-functional adaptations (resulting from evolutionary history) are necessarily involved in community assembly. It has been suggested that in this type of forest, facilitative interactions prevail under unfavorable environmental conditions (e.g. Espinosa et al., 2011, 2014). Using the plant's-eye perspective (Murrell et al., 2001), we focus on individual species and analyze the effect of each one on the structure of community diversity. We hypothesize that if facilitative interactions prevail, most or at least some key (i.e., nurse), species would experience higher taxonomic diversity in their close neighborhoods, whereas functional or phylogenetic diversity would not show any particular pattern. On the contrary, if other mechanisms such as competition based on niche differences or competition based on competitive ability differences are ruling community assembly, we expect FD (and PD) increasing or decreasing respectively in those neighborhoods (Table 1).

To test our hypothesis, we employ the Individual Species Area Relationship (ISAR; Wiegand et al., 2007). Analogously to the

proverbial Species-Area Relationship (Scheiner, 2003), the ISAR leads to estimate how species richness (i.e., TD) is spatially arranged around the individuals of a particular species. Using fully mapped communities and appropriate null models to control for the effects of environmental heterogeneity, the function ISAR(r) allows assessing the effects of particular species on, and their responses to, local TD at different spatial scales (i.e., at different radii r defining the neighborhoods; Wiegand et al., 2007). To assess the structure of FD and PD in the same plant neighborhoods, we use two analogous functions, i.e., the IFDAR(r) (Individual Functional Diversity–Area Relationship) and the IPSVAR(r) (Individual Phylogenetic Species Variability–Area Relationship). Contrasting ISAR, IFDAR and IPSVAR observations against the expectations of appropriate null models allows distinguishing ‘accumulators’ and ‘repellers’ of TD, FD and PD, i.e., species whose individuals are surrounded by higher and lower diversity than expected at a particular spatial scale, respectively (Wiegand et al., 2007). Both accumulation and repulsion of TD, FD and PD have been interpreted as evidences for non-neutral or niche-based processes that influence the distribution and diversity of tree species in forest communities (Wiegand et al., 2007; Espinosa et al., 2015; Wang et al., 2016) and shrublands (Chacón-Labela et al., 2016a, b). If diversity around the individuals of a target species does not deviate significantly from that expected, this is taken as evidence for neutrality (Wiegand et al., 2007; Espinosa et al., 2015). The prevalence of these plant types within a community (i.e., accumulator, repeller and neutral) and the spatial scales at which such effects occur could shed light on the biotic mechanisms implied in community assembly in mega-diverse communities (Table 1).

As the influence of environmental heterogeneity and dispersal limitation in the distribution of trees in this forest has been previously demonstrated (Jara-Guerrero et al., 2015), we test the observed ISAR, IFDAR and IPSVAR functions against the expectations of individual null models accounting for habitat filtering and stochastic processes. The joint use of the three functions, then, would allow assigning patterns to specific interactive mechanisms (Table 1). Thus, accumulator behavior in the ISAR function with neutral behavior for IPSVAR and IFDAR would indicate pure facilitation (e.g., as in a stressful environmental context where one or several “nurse species” expand habitat conditions in their neighborhood for other less tolerant species). However, if the accumulator behavior of ISAR is accompanied with accumulator behavior in IFDAR and/or IPSVAR, we could assume that the facilitator effect is combined with a limiting similarity mechanism (i.e., with competition based on niche-differences). On the contrary, an

Table 1

Interpretation of the biotic processes implied in the assembly of plant communities 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	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.
Neutral	Accumulator	Accumulator/Repeller	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.
Neutral	Repeller	Accumulator/Repeller	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.

accumulator species for ISAR which shows a repeller behavior for IFDAR and/or IPSVAR, indicates that its facilitative effect is accompanied by some competitive processes based on fitness differences (Mayfield and Levine, 2010) affecting the facilitated species (Table 1).

A repeller behavior for ISAR could be the consequence of competitive interactions with the focal species (i.e. only some species are able to occur in the vicinity of the target species) or among species facilitated by the focal species. If either IFDAR or IPSVAR functions (or both) show neutral behavior, the mechanism that could determine the taxonomic exclusion would probably be interference competition (Amarasekare, 2002) (Table 1). However, if combined with accumulator values for IFDAR or IPSVAR the competition would be mediated by limiting similarity. On the contrary, if IFDAR or IPSVAR show also repeller behaviors, that would indicate that only certain competitive functional patterns could thrive under the canopy or in the close vicinity; thus we could assume that competition among the focal species and its neighbors or among the facilitated neighbors is mediated by fitness differences. Of course, these combinations could vary depending on the existence (or not) and the prevalence of phylogenetic niche conservatism and possible evolutive convergence affecting the traits involved in the coexistence of individual species (Chacón-Labela et al., 2016a, b).

2. Material and methods

2.1. Study site

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

The climate is characterized by a rainy season with an average annual rainfall of 515 mm from January to April (wet season) and only 152 mm on average during the eight-month dry season (weather station Huaquillas for the period 1969–2014). The average temperature is 25.2 °C with a maximum variation of 3.4 °C between the coldest and warmest month. The lower temperatures occur during the dry season.

In the center of the REA, a square, 300 × 300 m (i.e., 9 ha) permanent plot (i) was installed in 2009, and all trees and shrubs with DBH ≥ 5 cm were tagged and identified at the species level. Average density (+ s.e.) of trees and shrubs in this area is (409 ± 17 trees/ha and 183 ± 48 shrubs/ha. During the dry season (July to September 2010 and 2011) tagged plants were mapped using a total station, Leica TS02-5 Power. The average canopy height of the forest in the plot is 15 m (Espinosa et al., 2015). The topography in the plot is quite flat, with some small depressions. Soil is mostly sandy loam. For the analysis of the effect of individual species on community diversity, we selected the 23 species (15 trees, 8 shrubs) with had more than 16 individuals (Table S1 in Supporting Information).

2.2. Functional trait collection

All the traits were measured following standardized protocols (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). We measured functional traits for all trees and shrubs in the permanent plot.

For each species, we randomly collected 10 sun leaves from each of 50 individuals, i.e., a total of 500 leaves by species. Leaves were collected during the phenologic peak. Leaf area (LS) was measured with the program Image J (Abràmoff et al., 2004; Kraft and Ackerly, 2010). Specific leaf area (SLA) was calculated as the fresh leaf area divided by the leaf dry mass (after 48 h drying at 80 °C). For species with compound leaves, the rachis was included in the measurements.

To estimate wood density (WD), we collected five secondary branches (with a circumference between 10–20 cm) for three individuals per species. Fresh wood volume was determined with the water displacement method (Chave et al., 2006), after which samples were oven-dried at 80 °C and weighed. When this was not feasible, we employed the Global wood density database of Chave et al. (2009) and Zanne et al. (2009). In this case, if there were several density measurements for a species, we calculated and used their mean. Maximum height (H_{\max}) was measured by using a compact Electronic Laser Hypsometer Tru-Pulse 360°, from the base to the uppermost tip of trees.

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

2.3. Phylogeny construction

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

2.4. Spatial pattern analyses

For each of the 23 target species, we first selected a spatial point process, compatible with its realized spatial pattern, to be used as a null model. In order to find the appropriate null model for each species, we followed an approach conceptually similar to the pattern reconstruction strategy of Wiegand and Moloney (2013), as implemented by Pescador et al. (2014) and Jara-Guerrero et al. (2015). To begin with, we fitted a battery of different spatial null models for each species: (1) a homogeneous Poisson process (HPP) with constant intensity λ equal to the density of the observed pattern in the map; (2) a homogeneous Poisson cluster process (HPCP) with constant intensity λ and parameters σ and ρ fitted by minimum contrast (Diggle, 2003); (3) inhomogeneous Poisson processes (IPP) with an intensity function $\lambda(x, y)$ estimated with a Gaussian kernel (Wiegand et al., 2007) with 13 different σ values (bandwidths), from $\sigma = 15$ to $\sigma = 75$ m in 5 m intervals; and, finally, (4) inhomogeneous Poisson cluster processes (IPCP) (Waagepetersen, 2007) with bandwidth-values similar to those considered for the IPPs. Then, to select the null model that best describes the spatial properties of each species, we computed the homogeneous (or inhomogeneous) K-function for the observed spatial pattern of the species and compared it to the average of the K functions of 199 simulations for each null model. The best model for each species was selected with the goodness-of-fit u statistic (Diggle, 2003; Loosmore and Ford, 2006; Pescador et al., 2014). K functions were computed from $r = 0$ to $r = 60$ m, with 1 m increments.

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

2.5. Individual diversity-area relationships

For each species we summarized the structure of the three community diversity components around the individuals of each species: TD using the ISAR function, FD with the IFDAR-function, and PD with the IPSVAR-function (De la Cruz, 2017). The $ISAR_t(r)$ function (Wiegand et al., 2007) estimates the expected number of species within circular areas with radius r around an average individual of a target species t . To calculate $ISAR_t(r)$, we first calculated the bivariate emptiness probability $P_{ij}(0, r)$ that species j was not present in circles with radius r around plants of the target species t (without counting the focal stem if $t = j$) and we then summed $1 - P_{ij}(0, r)$ for all species (N) present in the plot. ISAR was then estimated for each species t as follows:

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

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

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

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

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

where S is the total number of species, x_j is the abundance of species j in the community and z_j is the distance (usually Gowers distance) in the multivariate space of traits from species j to the centroid of the community (Laliberté and Legendre, 2010). In the same way, we estimated $IPSVAR_t(r)$, the expected phylogenetic species variability within circular areas with radius r around an average individual of the target species t as:

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

where $PSV_i(r)$ is the Phylogenetic Species Variability index (Helmus et al., 2007) computed for communities within circles of radius r around each i of n individuals of the target species. PSV quantifies how phylogenetic relatedness decreases the variance of a hypothetical unselected/neutral trait shared by all species in a community, so it is directly related to mean phylogenetic distance. Its expected value is 1 when all species in a sample are unrelated (i.e., a star phylogeny) and approaches zero as species become more related. It is computed as $1 - \bar{c}$, where \bar{c} is the average of the off-diagonal elements of the covariance matrix that summarizes the correlation structure of the community phylogeny (Helmus et al., 2007).

To avoid difficulties due to small sample size we only calculated functions for species with at least 16 individuals in the plot. All the individual species-area functions were computed from $r = 1$ to $r = 60$ m, with 1 m increments.

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

Deviations from the null model predictions were assessed with the Studentized maximum absolute difference (MAD) envelope test of Myllymäki et al. (2017) for three spatial scales, i.e., for three ranges of neighborhood radii: from 1 to 20 m, 21 to 40 m and 41 to 60 m. Species that showed significant positive or negative deviations from the null

model in any of these ranges were considered respectively as accumulators or repellers of diversity at such spatial scales. Species that did not show deviations from the null model at any of the three spatial ranges were considered as "neutrals". It is important to take into consideration that our null model approach eliminates the spatial signal due to the environmental heterogeneity at the corresponding scales leaving alone the effect of plant-to-plant interactions (Chase and Myers, 2011). All calculations were done using the R statistical software, version 3.1.0 (R Development Core Team, 2014). Null models were fitted using the packages *spatstat* (Baddeley et al., 2015) and *selectsp* (Jara-Guerrero et al., 2015). The $ISAR$, $IFDAR$ and $IPSVAR$ analyses were implemented using the package "idar" (De la Cruz, 2017), and the Studentized MAD envelope test using the package "sppptest" (Myllymäki et al., 2017).

3. Results

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

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

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

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

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

4. Discussion

The current scientific consensus suggests that the composition and local structure of a plant community is the result of stochastic and deterministic processes (HilleRisLambers et al., 2012), sometimes called "community assembly processes" (Götzenberger et al., 2011), acting together. Our results, based on an individualistic species

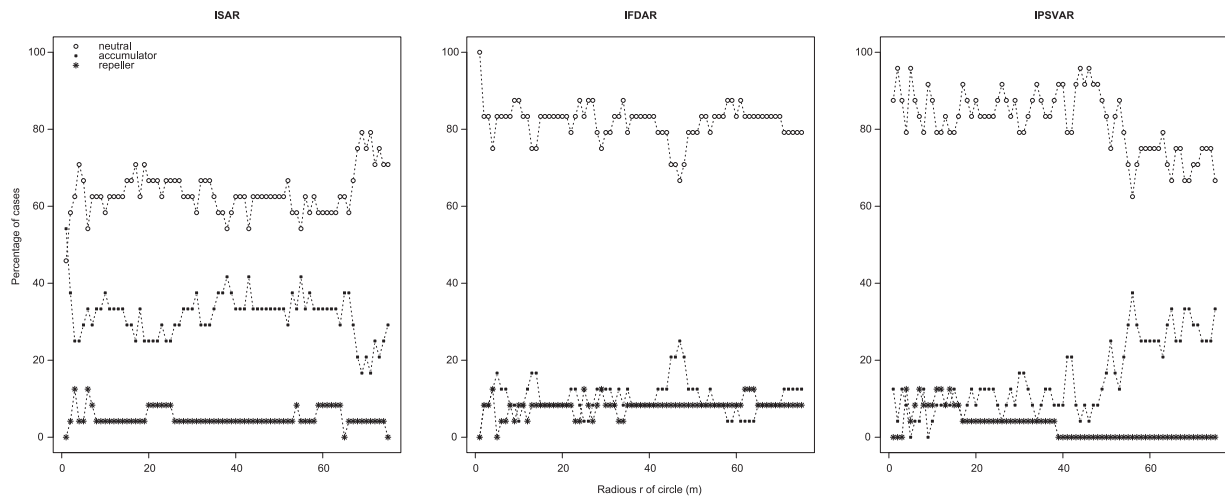


Fig. 1. Proportion of significant accumulator, repeller and neutral species for ISAR (Individual Species–Area Relationships), IFDAR (Individual Functional–Diversity–Area Relationship) and IPSVAR (Individual Phylogenetic –Area Relationship) in the REA, when considering different spatial scales (i.e.,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

approach, show clear evidences of several of these processes, including dispersal limitation, habitat filtering and plant-to-plant interactions (i.e. facilitation and competition) ruling community assembly in the southern Ecuadorian dry tropical forest of the REA. Confirming the findings of [Jara-Guerrero et al. \(2015\)](#) we found that 14 out of the 23 studied species were best described by IPCP processes, i.e., spatial processes including dispersal limitation. This is not surprising as the prevalence of dispersal limitation in tropical forests it is a well-known fact (i.e., [Condit et al., 2000](#)). All the best-fit spatial processes selected for the target species were also inhomogeneous, which suggest the relevance of environmental heterogeneity (i.e., habitat filtering) for community assembly. This result is especially relevant because it shows

that the effects of environmental heterogeneity vary within the relative small scale of the plot (9 ha), in contrast with the extended view, within the general framework of modern coexistence theory, that the habitat filters the regional species pool at coarser scales ([Cornwell and Ackerly, 2009](#)), i.e., at scales coarser than those where the effects of species interactions take place. Although the effects of environmental heterogeneity at finer scales is a well-known fact within the ecological point pattern literature (e.g., [Wiegand and Moloney, 2014](#)), only recently this idea is permeating other ecological fields ([Chase, 2014](#)).

Since dry forests occur in harsh environments dominated by water shortages and pronounced seasonality in precipitation, it is frequently assumed that facilitative interactions would be the norm and influence

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 significant deviations from the null model (after accounting for the false discovery rate) and therefore accumulator or repeller behavior. Grey background: species that behaved as accumulators in the evaluated range. Black background: species that behaved as repellers in the evaluated range. Neutral behavior is showed as white cells. ISAR (Individual Species–Area Relationship), IFDAR (Individual Functional–Diversity–Area Relationship) and IPSVAR (Individual Phylogenetic Species Variability –Area Relationship).

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>Erythroxylum 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

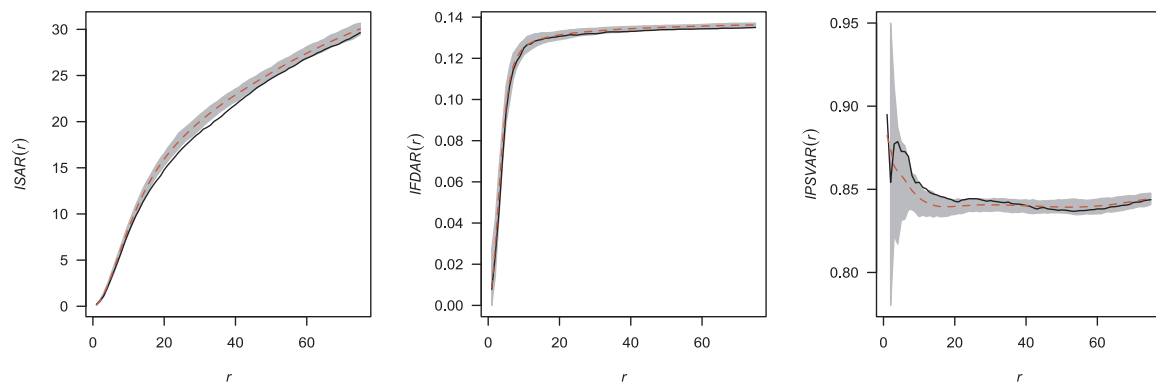


Fig. 2. Test of the individual diversity–area functions against the null model for *Chloreucon mangense* (a) ISAR (Individual Species–Area Relationship) (b) IFDAR (Individual functional-diversity–area relationship). The black line represent the observed function and the grey areas correspond to the envelopes computed from 199 simulations of *Chloreucon mangense* patterns from the null model. The red dashed line represents the expectations from the null model (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

community structure and composition (Espinosa et al., 2013, 2015). Our main hypothesis was that facilitative processes would be prevalent among species interactions in the REA dry forest. In agreement with this prediction, we found that a large number of species (11 out of 23) showed accumulative behavior for ISAR (i.e., more TD than expected) at fine scales (1–20 m). This is the spatial range where the direct effects of interactions among individual plants could be expected and detected (Hubbell, 2001; Uriarte et al., 2004). The accumulation of TD at short spatial scales in environments where abiotic stress is prevalent it has been interpreted as a consequence of the effect of some individual species (i.e. nurse species) expanding the habitat requirements of other species in their neighborhood (Chacón-Labelle et al., 2014; Espinosa et al., 2015). In the REA, however, this interpretation should be re-considered cautiously on a per-species basis since some of the accumulators of TD in our study are also fine-scale accumulators of FD or PD (see Table 2). The increase of FD in a community, with values larger than expected for a null model of community assembly, is usually considered evidence of the effect and prevalence of competition (i.e., limiting similarity; Cornwell et al., 2006; Kraft and Ackerly, 2010). It seems, therefore, that the enhancement of environmental conditions, which allows an increase of TD in these cases, goes together with the establishment of strong competitive processes within the ameliorated microhabitats. This joint effect of facilitation and limiting similarity within enhanced patchy habitats has been reported in other ecosystems, such as dry alkali grasslands (Kelemen et al., 2015), where trait diversity among the facilitated species was found to increase with the biomass of the nurse species. In the REA, this effect is mediated by both trees (*Jacquinia sprucei*, *Tabebuia billbergii*) as well as by shrubs (*Achatocarpus pubescens*, *Malpighia emarginata*) so the biomass explanation does not apply here. On the other hand, there are also trees and shrubs among the eight neutral species, so plant life form does not seem to be implied in these mechanisms.

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

Only one species showed repeller behavior for TD at fine scales, i.e., *Chloroleucon mangense*. Previous studies about the effects of individual species on TD have interpreted the existence of repeller species as the result of competitive processes (e.g., a focal repeller species interfering

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

Almost a third of the studied focal species (8 species) showed neutral behavior for TD, FD and SD at fine scales. Although a first interpretation could try to explain this results as a consequence of species depending only on stochastic mechanisms and habitat filtering (which we accounted for with the null models), recent theoretical developments predict that in species-rich communities, stochastic dilution effects, i.e., pure geometrical mechanisms caused by the high number of species, would blur non-random patterns generated by competitive or facilitative interactions (Wang et al., 2016).

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

Our framework, which is based on the use of null models reproducing processes of sound ecological sense, can be easily extended to other diversity metrics than can help to shed light on coexistence process by considering the individual species perspective simultaneously at many spatial scales. For instance, in our Neotropical dry forest the apparent

dominance of neutral processes and facilitation after surveying only TD (Espinosa et al., 2015) turned to non-neutral prevalence when the other diversity components are evaluated simultaneously.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ppees.2018.07.004>.

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