Study of the floristic, functional and phylogenetic composition of trees in a short time in a forest fragment of the Atlantic Forest, Brazil

Estudio de la composición florística, funcional y filogenética de árboles en poco tiempo en un fragmento de bosque del bosque atlántico, Brasil

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SUMMARY

Discrete thresholds of structural or functional decline of a vegetation type are not readily apparent, as a vegetation type can slowly decline leading to transformations in its species composition and weakened or altered functions. However, forest monitoring can be used to assess changes in ecological functions in community structure and functional and phylogenetic composition of species. This study evaluated the existence of temporal variations in the functional and phylogenetic composition of a tree community, the occurrence of heterogeneity in the behavior of phylogenetic and functional variations, and how this possible heterogeneity influences the functional and phylogenetic variations under the aspect of environmental variations and by demographic ecological processes. Results detected quantitative and qualitative changes throughout the community, such as colonization, local extinctions, in demography and biomass, and increased evolutionary distinction, lower wood density species and phylogenetic clustering. These results have shown us that the natural changes of a community should not be underestimated, because the disappearance of a community can not only occur by the direct elimination of vegetation, but can be incremental with gradual changes in its functional characteristics and species composition, transforming itself into a new community with a new combination of species and new functions.

Key words: functional attributes, forest ecology, Atlantic forest, phylogeny, forest dynamics.

RESUMEN

Los umbrales discretos de deterioro estructural o funcional de un tipo de vegetación no son fácilmente aparentes, ya que un tipo de vegetación puede disminuir lentamente, lo que lleva a transformaciones en la composición de sus especies y funciones debilitadas o alteradas. Sin embargo, las observaciones pueden usarse para evaluar los cambios en las funciones ecológicas antes de que esto ocurra a través de la estructura comunitaria y la composición funcional y filogenética de las especies. Este estudio evaluó la existencia de variaciones temporales en la composición funcional y filogenética de una comunidad arbórea; la ocurrencia de heterogeneidad en el comportamiento de variaciones filogenéticas y funcionales; y cómo esta posible heterogeneidad influye en las variaciones funcionales y filogenéticas bajo el aspecto de variaciones ambientales y por procesos demográficos ecológicos. Los resultados en la detección de cambios cuantitativos y cualitativos en toda la comunidad con la colonización y las extinciones locales en la comunidad, las diferencias demográficas y de biomasa, la distinción evolutiva aumentada, las especies de menor densidad de madera y el agrupamiento filogenético. Los resultados han demostrado que los cambios naturales de una comunidad no deben subestimarse, porque la desaparición de una comunidad no solo puede ocurrir por la eliminación directa de la vegetación, sino que puede ser incremental con cambios graduales en sus características funcionales y composición de especies, transformando en una nueva comunidad con una nueva combinación de especies y nuevas funciones.

Palabras clave: atributos funcionales, ecología forestal, bosque atlántico, filogenia, dinámica forestal.

INTRODUCTION

Knowledge about the worldwide conservation status of biodiversity, as well as its human use, has faced a growing demand worldwide, which has been driving increasing support for strategies of natural resource management, nature protection and sustainable resource use. The perception and quantification of biodiversity change over time

are nonetheless a great challenge, especially when gradual, low-intensity changes are observed within short timespans in a local or regional geographic range. The lack of temporal studies on this matter prevents the assessment of the actual status of biodiversity (Del Vecchio *et al.* 2016).

Changes in biodiversity may encompass more than species richness decline, but entails alterations in the identity of species and, potentially, in community function (Hillebrand *et al.* 2018). From the human perspective, these shifts can hamper the provision of ecosystem services such as food sources, fuel, structural materials, medicines and genetic resources (Chapin *et al.* 2000). The abundances of species that control ecosystem processes may also be compromised, leading to further compositional changes in the community and, consequently, increasing vulnerability to species invasion (Navarro et al. 2017). Although the reduction in species distribution may be detected with relative ease, discrete thresholds of structural or functional decline are not easily perceptible (Del Vecchio *et al.* 2016).

According to a recent study, since the year 1900, seed plants have been extinguishing by a rate of approximately three species per year, with emphasis on island and wet tropics floras (Humphreys *et al.* 2019). In Brazil, the greatest loss has occurred in the south-eastern region where the Atlantic Forest vegetation predominates, with 21 to 30 species becoming extinct within the last 119 years (Humphreys *et al.* 2019). For its high biological relevance and anthropogenic threats faced by its highly endemic flora, the Atlantic Forest is considered a hotspot of biodiversity (Ribeiro *et al.* 2009). The broad range of agricultural land uses and lack of an efficient forest management plan threaten the Atlantic Forest remnants (Becker *et al.* 2013), specifically in Mantiqueira Range (*Serra da Mantiqueira*), inserted in a densely populated area that neighbors large cities like Rio de Janeiro and São Paulo. One of the main issues concerning Atlantic Forest conservation is the intense fragmentation process that it has undergone since the beginning of colonization in the sixteenth century, which resulted in its occurrence being currently restricted to small scattered fragments (Ribeiro *et al.* 2009).

Wet tropical regions are characterized by high annual rainfall and high evapotranspiration rates, with drought being an important driver of diversity patterns and survival of species in tropical forests (Esquivel-Muelbert *et al.* 2017). However, with the likely changes in precipitation regimes promoted by climate change, many plant species may not be able to adapt fast enough nor to track suitable habitats in terms of water availability (Esquivel-Muelbert *et al.* 2017). Moreover, in a given ecosystem, niche opportunities that stem from climatic fluctuations over time can determine which species will be able to occupy these novel niche dimensions and which functions may be provided or lost (Pulla *et al.* 2017, Maia *et al.* 2020). Such niche opportunities can explain changes in species composition and forest productivity, as well as species colonization and occupation strategies (Pulla *et al.* 2017).

In view of all this context, it is important to note that in 2010, the Parties to the Convention on Biological Diversity adopted the Strategic Plan for Biodiversity 2011-2020 and its 20 associated Aichi Biodiversity Targets. Aichi Biodiversity Target 19 refers specifically to knowledge, values, functioning, situations and trends about biodiversity through its monitoring. Although long term studies are important for monitoring the conservation status of biodiversity in vegetation fragments, detecting changes in shorter periods offers interesting possibilities to observe more specific changes in the taxonomy, phylogeny, structure and functions of the community, as well as interactions between them. Importantly, these short-term assessments of biodiversity change may serve as an alert before detrimental and irreversible alterations occur.

We, field researchers, were able to see in the surveys that even in a short period of time, forest communities have been reflecting perceptible changes in their physiognomy. And for that, we tested the following hypothesis: Over a period of six years, are the changes that occur in the community due to the effect of demographic fluctuations able to reflect on ecological functions and alter the phylogeny of a community? To explore this hypothesis, this study seeks to relate: (i) if taxonomic composition changed between the intervals (controlling soil effects) and (ii) if taxonomic composition, along with community dynamics, phylogenetic diversity shifts and soil, leads to shifts in community structure, community function, above-ground woody biomass and evolutionary distinctiveness.

METHODS

Study area. This study was carried out in an area inserted in the Atlantic domain, in Mantiqueira Range (*Serra da Mantiqueira*, in Portuguese), south-east Brazil. The studied forest fragment is named *Mata dos Gnomos* (Gnome Woods, in free translation) and is located in a private natural heritage reserve (RPPN Altomontana) in the Municipality of Itamonte, Minas Gerais State (figure 1). *Mata dos Gnomos* is a semideciduous forest disjunction inserted in a matrix of ombrophilous forests (Oliveira-Filho 2009), and its altitude ranges from 1,445 to 1,495 m.

The climate of the region is Cwb according to the Koppen classification, mesothermic with dry winters (June-July) and rainy with mild summers (December-January). The temperature varies from 17.4 °C to 19.8 °C, not exceeding 22 °C, and average annual rainfall is 1,749 mm. The fragment has been under protection as a private natural heritage reserve for about 80 years, with presence of some remaining old trails inside the forest, which has presence of the Brazilian pine *Araucaria angutistifolia* (Bertol.) Kuntze. Adjacent to this fragment, there are ecotonal areas: one of them with monodominance of bamboo and another with dominance of candeia (*Eremanthus erythropappus* (DC.) MacLeish).

To better analyze the behavior of precipitation, and thus be able to infer about changes in precipitation over time,

we took the precipitation data in the interval from 2005 to 2017. This analysis was made only to set up a scenario of rainfall distribution over time, to help in understanding the behavior of the forest under study. The study area had a rainfall coefficient of variation of 21.27 % and its annual rainfall profile is displayed in figure 2.

Data collection. In 2011, 22 plots of 400 m² were established along five transects, spaced 10 m apart. All arboreal individuals with diameter at breast height (DBH) ≥ 5 cm within these plots were measured. For trees with multiple stems, we included those of which the square-root of the sum of squares of each stem DBH met the inclusion criterion (DBH ≥ 5 cm). The plots were resurveyed in 2017 and all surviving trees were re-measured. New individuals that reached the inclusion criterion (recruits, DBH ≥ 5 cm) were identified to the species level, measured in terms of DBH and height and marked with numbered aluminum tags, while dead individuals were also recorded.

In each plot, one soil sample was collected at a depth of 0 to 10 cm to characterize soil physical and chemical aspects. The following attributes were assessed: aluminum,
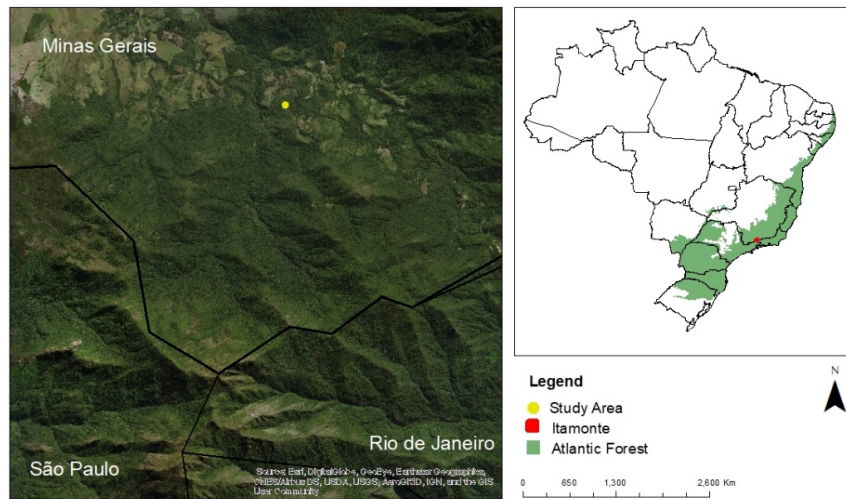

Figure 1. Study area location (Itamonte) in Minas Gerais State, Brazil, and Brazilian biogeographic domain of area.

Ubicación del área de estudio (Itamonte) en el estado de Minas Gerais, Brasil, y el dominio biogeográfico brasileño del área.
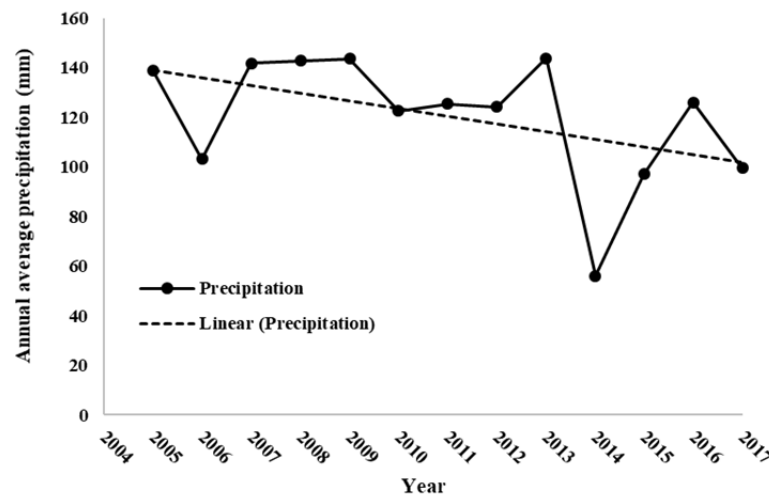

Figure 2. Total annual precipitation from 2004 to 2017 in the study region of Itamonte, Minas Gerais State, Brazil. Data obtained from Instituto Nacional de Meteorologia (INMET)-BDMEP database, collected from the meteorological station of São Lourenço Municipality.

Precipitación total anual de 2004 a 2017 en la región de estudio de Itamonte, estado de Minas Gerais, Brasil. Datos obtenidos de la base de datos del Instituto Nacional de Meteorología (INMET) -BDMEP, recopilados de la estación meteorológica del municipio de São Lourenço.

sum of bases, organic matter, pH in water and sand, silt and clay proportions (dag/kg) to characterize soil texture.

Tree identification followed APG IV and was performed in the field, or else by consulting experts or the ESAL Herbarium at the Federal University of Lavras (UFLA). Species nomenclature followed The Plant List database (theplantlist.org) in case synonyms were eventually recorded.

 From the species abundance matrix and using the *vegan* package (Oksanen *et al.* 2018), we performed a Detrended Correspondence Analysis (DCA) using data from both inventories to synthesize differences in taxonomic composition among plots (*i.e.* beta diversity).

Biomass and productivity were calculated following the methodology described by Poorter *et al.* (2017), assuming that biomass stocks and dynamics are key ecosystem functions because biomass largely mediates local and global biogeochemical cycles in carbon, nutrients and water (Chapin *et al.* 2000). Productivity was obtained by the difference in the biomass between the inventories (biomass of the last year minus the biomass of the first year).

Obtaining variables of interest. Variables, aimed at describing the functional composition of each sample unit at each data collection year, were obtained through the community weighted means (CWMs) of the following attributes: wood density (WD), obtained from the Global Wood Density Database through values for species or averages of the genus or family (Chave *et al.* 2009); sprouting intensity (Spr intensity - %), obtained by the ratio between the number of stems and the number of individuals; sprouting frequency (number of individuals that have more than one stem/ number of individuals – Spr frequency - %); and species' maximum DBH (cm). The CWM values were calculated with the R function *functcomp* from the FD package v. 3.5.2 (2018) (Laliberté *et al.* 2014). The Evolutionary Distinctiveness (ED) metric was obtained for each species by dividing the total phylogenetic diversity of a clade among its members, applying a value to each branch equal to its length divided by the number of species belonging to the branch; species with no close relatives have high ED values, and a community with high ED values is considered to have more evolutionarily unique species (Edwards *et al.* 2017). We also calculated the CWM of this metric to obtain a single value of evolutionary distinctiveness for each sample unit. For each measurement year, we calculated the standardized effect sizes (SES) of phylogenetic diversity (PD), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), aiming at neutralizing the bias caused by variations in species richness across sample units. We used the packages V.PhyloMaker (Jin and Qian 2019), PhyloMeasures (Tsirogiannis and Sandel 2016) and the mega angiosperm tree GBOTB.extended to build our tree and obtain the metrics of ED diversity and phylogenetics.

Based on the abundances of dead individuals and recruits, we calculated the annual mortality and recruitment rates as proposed by Sheil *et al.* (1995). The above-ground

woody biomass (AGWB, in Mg) of dead individuals (AGWBdead) and of recruits (AGWBrec) was also calculated to evaluate the demographic fluctuations by changes in biomass and not only through changes in species abundances (Sheil *et al.* 1995). Biomass was obtained through the BIOMASS package (Rejou-Mechain *et al.* 2017), using the modified equation of Chave *et al.* (2014). We used equation with parameters for DBH, wood density and E, which is related to climate stress and predicts tree height when it is absent in the data. This equation has been developed and has been widely applied in rain forests, although with uncertain expectations when applied to other vegetation types. We calculated the temporal beta diversity for each sample unit using the squared distances between the coordinates of the plots in DCA axis 1 in the first census and in the second census. Only the DCA axis 1 was used in the analysis due to its eigenvalue of 0.45 against 0.22 from axis 2. The soil variables were synthesized in two explanatory summary variables represented by the value of each sample unit on the two first axes of a Principal Component Analysis (PCA) performed with all the collected soil variables (figure S1).

Data analyses. All analyses were performed in the environment R version 3.6.1 (R Core Team 2019), adopting the significance level of 5 % for all analyses.

Two matrices were used to test the change in species composition and functional attributes over time, each containing data from one of the inventories. We performed non-metric multidimensional scaling (nMDS) for the difference in species composition among sample units using Bray-Curtis dissimilarity. We used the Procrustes and ProTest analyses in both cases. The most commonly used method for Procrustean fit is based on the least squares criterion that minimizes the sum of square residuals (m) between the two configurations. The analyses were implemented using the vegan package.

Three main analyses were conducted with all the variables of interest regarding taxonomic composition, functional composition and phylogenetic diversity (DCA axis 1, CWM WD, AGWB, CWM sprouting frequency, CWM sprouting intensity, CWM maximum DBH and CWM evolutionary distinctiveness), as well as demographic variables (mortality and recruitment rates); AGWB of mortality, recruitment and productivity, environmental variables (edaphic PCA axes 1 and 2), and phylogenetic diversity variables (sesPD, sesMPD and sesMNTD). First, we tested if the taxonomic composition (Procrustes and DCA axis 1), functional composition (CWMs) and phylogenetic diversity metrics differ between the censuses and if its relationship with soil and taxonomic composition (except for DCA axis 1) shifted across the censuses. For this, we used Generalized Linear Mixed Effects Models (LMM). Plot was used as random factor because of the repeated measures at the same plot.

We, afterwards, evaluated if there are differences between the inventories in the mortality and recruitment rates and in the AGWB of recruitment and mortality through

LMM. Finally, we also assessed potential relationships between the temporal variation of functional composition, community structure/dynamics and phylogenetic diversity with demographic, phylogenetic diversity variation, taxonomic composition shifts and edaphic variables. To do so, we obtained the percentage variation of the CWM of each attribute ([(CWM year 2 - CWM year 1) / CWM year 1] * 100) and for productivity (AGWB year 2 minus AGWB year 2) as a function of demographic variables (mortality, recruitment, AGWB of dead and AGWB of recruits), species substitution (DCA axis 1 squared distances), edaphic (PC1 and PC2) and variation in phylogenetic diversity (Δ ses PD, Δ ses MPD and Δ ses MNTD, between years). In this case we used linear models (LM).

In the modelling approach we built a global model containing all the variables and dredged it to obtain models with all combinations of a maximum of two variables (due to the reduced number of observations) and which correlate by less than | 0.6 |. The models obtained with Δ AICc less than or equal to 2 in relation to the best model were submitted to a multi-model inference, using the "model. avg" function of "MuMIn" package (Bartón 2009) to capture the uncertainty of the effects of all predictors on the response variables, so that the coefficients were averaged and significant values were obtained. All variables were worked within the Gaussian distribution family, assuming the criteria of residual normality (Shapiro-Wilk test) and absence of spatial autocorrelation in the global model by the ncf package correlog function (Bjørnstad 2008).

The variables, together with the analyses used and their functions, are found in a summary table1.

RESULTS

Overall, a total of 139 species were recorded: 135 species in the first inventory year (2011) and 131 in the second year (2017). In the first measurement, 1304 individuals with a total AGWB of 282.3 Mg (density of 1552 individuals/ha; AGWB of 336.07 Mg/ha) were recorded, whereas in the second measurement, 1189 individuals summing up 281.1 Mg of AGWB (density of 1415 individuals/ha AGWB of 334.64 Mg/ha) were recorded. Mortality was significantly higher than recruitment through the six-year time span (figure 3).

Qualitative differences were identified in terms of the balance between recruitment and mortality for a few species between inventory years – *e.g.* mortality but no recruitment of *Tachigali rugosa* (Mart. ex Benth.) Zarucchi *et* Pipoly and *Solanum leucodendron* Sendtn. There were species that disappeared from the community and species that arrived in the community (*e.g. Cyathea delgadii* Sternb). Other species, like *Leandra melastomoides* Raddi, entered the community (table 2). The Procrustes for the nMDS

Table 1. Summary table with the variables used and their respective analyses and classification regarding the topic addressed.

Resumen de las variables utilizadas y sus respectivos análisis y clasificación con respecto al tema abordado.

| Variables		Abbreviation	Analyses	Classification
Species composition			nMDS; Procrustes and ProTest; DCA	Taxonomic and functional
Soil texture			PC2	Taxonomic
Evolutionary distinctiveness		ED	LMM	Phylogenetic
Community weighted means	Wood density	CWM WD	CWM WD	Functional
	Sprouting intensity	CWM Sprouting	CWM Sprouting	
	Sprouting frequency	CWM Spr Freq	CWM Spr Freq	
	Maximum DBH	CWM Max DBH	CWM Max DBH	
	Evolutionary distinctiveness	CWM ED	CWM ED	
Standardized phylogenetic diversity		sesPD	LMM	Phylogenetic
Standardized mean distance of pairs		sesMPD	LMM	Phylogenetic
Standardized average distance from the nearest taxon		sesMNTD	LMM	Phylogenetic
Demographic	Mortality rate		LMM	Taxonomic and functional
	Recruitment rate		LMM	
	Above-ground woody biomass	AGWB	LMM	
	Above-ground woody biomass of dead individuals	AGWBdead	LMM	
	Above-ground woody biomass of recruits	AGWBrec	LMM	
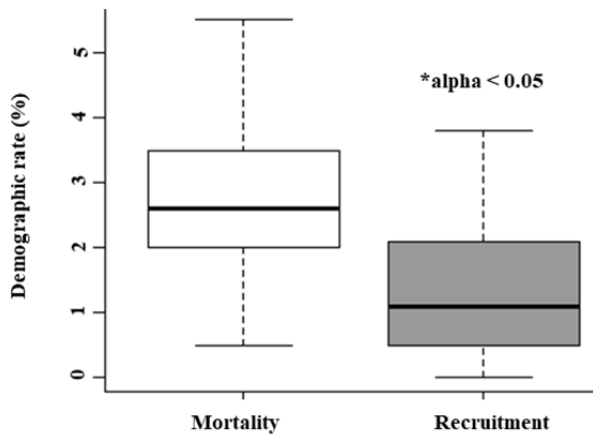
Figure 3. Mortality (%) and recruitment (%) of individuals observed between inventories for the sample units of the upper montane semi-deciduous tropical forest.

Mortalidad (%) y reclutamiento (%) de individuos observados entre inventarios para las unidades de muestra del bosque tropical montano superior.

and CWM values corroborated these floristic differences (figure 4). The graphical description of the Procrustes and ProtTest analyses (figure 4) indicated that there occurred changes in species composition (Procrustes m² = 0.3618; ProTest 0.7989, $P < 0.0001$) and functional traits (Procrustes m² = 0.3189; ProTest 0.8253, $P < 0.0001$) of the sample units in the six-year period covered. The DCA axis 1 scores showed significant differences between the communities sampled in 2011 and 2017 ($P = 0.01$), indicating that the taxonomic composition changed in the interval. Both variables related to sprouting differed significantly between censuses (2011 and 2017) and were strongly affected by species composition (DCA axis 1) ($P < 0.001$ for both). The CWM of maximum diameter showed a significant relationship with soil (PC2) ($P < 0.001$), with decrease in soil effect over this response variable between inventory years (figure 5A). The CWM of evolutionary distinctiveness only displayed significant relationships with the interaction between species composition (DCA axis 1) and year 2, in a way that the effect of species composition on evolutionary distinctiveness CWM increased in the second inventory (figure 5B). This indicates that the evolutionary
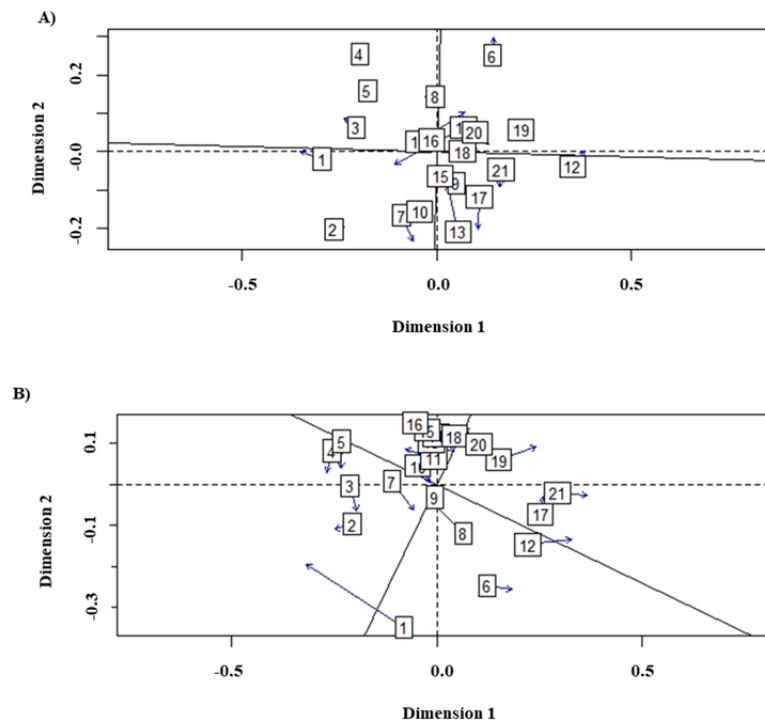

Figure 4. Procrustes Graph generated from (A) nMDS results and (B) CWM values. The numbers represent the sample units. The distance between the two inventories is the residual of Procrustes. Longer arrows indicate residuals with higher values (*i.e.* a larger difference in species composition/CWM between a pair of samples). The numbers are equivalent to the plots, the arrows indicate the direction and size of the change.

Gráfico de Procrustes generado a partir de (A) resultados de nMDS y (B) valores de CWM. Los números representan las unidades de muestra. La distancia entre los dos inventarios es el residuo de Procrustes. Las flechas más largas indican residuos con valores más altos (es decir, una diferencia mayor en la composición de especies/CWM entre un par de muestras). Los números son equivalentes a los gráficos, las flechas indican la dirección y el tamaño del cambio.
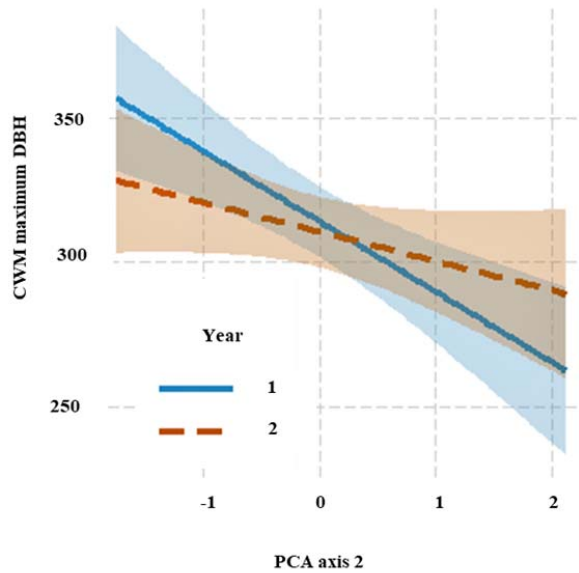
Figure 5. Relationships of temporal shift community-weighted mean (CWM) of: (A) maximum diameter (DBH maximum) with the soil (PC2), (B) evolutionary distinctiveness (ED) with species composition (DCA). The shades are the confidence bands of the fitted lines.

Relaciones del cambio temporal media ponderada por la comunidad (CWM) de: (A) diámetro máximo (DBH máximo) con el suelo (PC2); (B) distinción evolutiva (ED) con la composición de especies (DCA). Las sombras son las bandas de confianza de las líneas ajustadas.
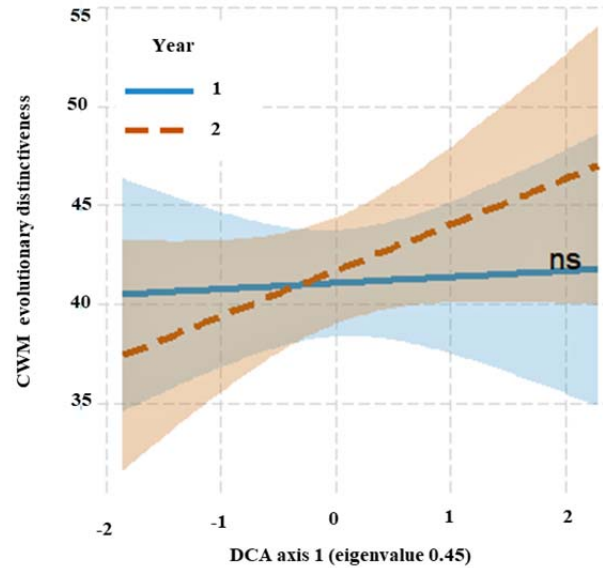
Figure 6. Relationships of temporal shift community- weighted mean (CWM) of evolutionary distinctiveness (ED) with species composition (DCA).The shades are the confidence bands of the fitted lines.

Relaciones de cambio temporal ponderadas por la comunidad media (CWM) de distinción evolutiva (ED) con composición de especies (DCA). Las sombras son las bandas de confianza de las lÌneas ajustadas.

Table 2. Table with the floristic balance of the 6-year interval with its respective evolutionary distinction value. Code: ● dead and no recruits. NA-These species did not have their ED calculated due to the name being under review.

Balance florístico del intervalo de seis años con su respectivo valor de distinción evolutiva. Código: ● muertos y sin reclutas. NA: estas especies no tenían su ED calculado debido al nombre que se estaba revisando.

Species	Family	ED	2011	2017
Alchornea glandulosa Poepp. *et* Endl. ●	Euphorbiaceae	47.51	X	X
Alchornea triplinervia (Spreng.) Müll.Arg.	Euphorbiaceae	47.51	X	X
Allophylus puberulus (Cambess.) Radlk.	Sapindaceae	55.49	X	X
Amaioua intermedia Mart. ex Schult. *et* Schult.f.	Rubiaceae	59.78	X	X
Annona cacans Warm. ●	Annonaceae	43.40	X	X
Annona emarginata (Schltdl.) H. Rainer	Annonaceae	43.40	X	X
Araucaria angustifolia (Bertol.) Kuntze ●	Araucariaceae	325.5	X	X
Aspidosperma australe Müll.Arg.	Apocynaceae	43.99	X	X
Aspidosperma olivaceum Müll.Arg. ●	Apocynaceae	43.99	X	X
Blepharocalyx salicifolius (Kunth) O. Berg	Myrtaceae	33.94	X	X
Byrsonima laxiflora Griseb.	Malpighiaceae	NA	X	X
Cabralea canjerana (Vell.) Mart. ●	Meliaceae	52.82	X	X
Calyptranthes grandiflora O. Berg	Myrtaceae	28.42	X	X
Calyptranthes widgreniana O. Berg ●	Myrtaceae	28.42	X	X
Campomanesia guaviroba (DC.) Kiaersk.	Myrtaceae	27.79	X	X

Continue

Table 2 Continued

Campomanesia guazumifolia (Cambess.) O. Berg ●	Myrtaceae	27.79	X	X
Campomanesia xanthocarpa (Mart.) O. Berg ●	Myrtaceae	27.79	X	X
Casearia decandra Jacq.	Salicaceae	44.79	X	X
Casearia mariquitensis Kunth	Salicaceae	44.79	X	X
Casearia sylvestris Sw.	Salicaceae	44.79	X	X
Cinnamomum glaziovii (Mez) Kosterm.	Lauraceae	19.69	X	X
Clethra scabra Pers. ●	Clethraceae	98.01	X	X
Cyathea delgadii Sternb.	Cyatheaceae	390.70	X	
Cybianthus peruvianus (A.DC.) Miq. ●	Primulaceae	40.61	X	X
Cybistax antisyphilitica (Mart.) Mart. ●	Bignoniaceae	37.18	X	X
Dalbergia frutescens (Vell.) Britton	Fabaceae	73.57	X	X
Daphnopsis coriacea Taub.	Thymelaeaceae	60.35	X	
Daphnopsis utilis Warm.	Thymelaeaceae	60.35	X	X
Dendropanax cuneatus (DC.) Decne. *et* Planch.	Araliaceae	57.42	X	X
Dictyoloma vandellianum A.Juss.	Rutaceae	74.24	X	X
Diplotropis ferruginea Benth.	Fabaceae	65.50	X	X
Eremanthus erythropappus (DC.) MacLeish ●	Asteraceae	30.92	X	X
Eugenia hiemalis Cambess.	Myrtaceae	31.67	X	X
Eugenia sonderiana O. Berg	Myrtaceae	31.67	X	X
Euplassa legalis (Vell.) I.M.Johnst.	Proteaceae	50.91	X	
Euplassa rufa (Loes.) Sleumer ●	Proteaceae	50.91	X	X
Ficus enormis Mart. ex Miq.	Moraceae	77.84	X	X
Laplacea fruticosa (Schrad.) Kobuski	Theaceae	98.45	X	X
Guapira opposita (Vell.) Reitz ●	Nyctaginaceae	122.00	X	X
Guatteria australis A.St.-Hil. ●	Annonaceae	42.99	X	X
Guatteria villosissima A.St.-Hil.	Annonaceae	42.99	X	X
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae	37.18	X	X
Ilex brevicuspis Reissek	Aquifoliaceae	105.70	X	
Jacaranda macrantha Cham.	Bignoniaceae	27.68	X	X
Jacaranda puberula Cham. ●	Bignoniaceae	27.68	X	X
Jacaranda subalpina Morawetz	Bignoniaceae	27.68	X	X
Lamanonia ternata Vell. ●	Cunoniaceae	100.40	X	X
Leandra aurea (Cham.) Cogn. ●	Melastomataceae	15.81	X	X
Leandra melastomoides Raddi	Melastomataceae	16.44		X
Leandra quinquedentata (DC.) Cogn. ●	Melastomataceae	15.81	X	X
Leucochloron incuriale (Vell.) Barneby *et* J.W.Grimes	Fabaceae	65.65	X	X
Matayba guianensis Aubl. ●	Sapindaceae	55.47	X	X
Maytenus gonoclada Mart.	Celastraceae	45.28	X	X
Maytenus ilicifolia Mart. ex Reissek	Celastraceae	37.89	X	X
Maytenus robustoides Loes.	Celastraceae	45.28	X	X
Maytenus salicifolia Reissek	Celastraceae	37.89		X

Continue

Table 2 Continued

Miconia cabussu Hoehne	Melastomataceae	17.89	X	X
Miconia chartacea Triana ●	Melastomataceae	13.69	X	X
Miconia cinnamomifolia (DC.) Naudin ●	Melastomataceae	15.60	X	X
Miconia corallina Spring	Melastomataceae	13.69	X	
Miconia latecrenata (DC.) Naudin	Melastomataceae	15.60	X	X
Miconia pusilliflora (DC.) Naudin	Melastomataceae	15.56		X
Miconia sellowiana Naudin ●	Melastomataceae	15.56	X	X
Miconia willdenowii Klotzsch ex Naudin	Melastomataceae	13.82	X	X
Mollinedia argyrogyna Perkins	Monimiaceae	108.70	X	X
Myrcia fenzliana O.Berg	Myrtaceae	27.85	X	X
Myrcia guianensis (Aubl.) DC. ●	Myrtaceae	27.43	X	X
Myrcia multiflora (Lam.) DC.	Myrtaceae	27.10	X	X
Myrcia obovata (O.Berg) Nied.	Myrtaceae	27.85	X	X
Myrcia pulchra (O.Berg) Kiaersk.	Myrtaceae	27.12	X	X
Myrcia splendens (Sw.) DC.	Myrtaceae	27.10	X	X
Myrcia venulosa DC.	Myrtaceae	27.85	X	X
Myrciaria floribunda (H.West ex Willd.) O.Berg	Myrtaceae	32.10	X	
Myrsine lineata (Mez) Imkhan.	Primulaceae	39.90	X	X
Myrsine umbellata Mart.	Primulaceae	39.90	X	X
Nectandra grandiflora Nees ●	Lauraceae	14.31	X	X
Nectandra nitidula Nees	Lauraceae	14.31	X	
Nectandra oppositifolia Nees	Lauraceae	14.40	X	X
Ocotea aciphylla (Nees et Mart.) Mez ●	Lauraceae	16.39	X	X
Ocotea corymbosa (Meisn.) Mez	Lauraceae	15.88	X	X
Ocotea diospyrifolia (Meisn.) Mez	Lauraceae	16.36	X	X
Ocotea indecora (Schott) Mez	Lauraceae	16.39	X	X
Ocotea minarum (Nees *et* Mart.) Mez	Lauraceae	17.14	X	X
Ocotea odorifera (Vell.) Rohwer	Lauraceae	16.62	X	X
Ocotea puberula (Rich.) Nees	Lauraceae	15.73	X	X
Ocotea pulchella (Nees et Mart.) Mez	Lauraceae	15.73	X	X
Ormosia fastigiata Tul. ●	Fabaceae	65.50	X	X
Ouratea floribunda (A.St.-Hil.) Engl. ●	Ochnaceae	98.81	X	X
Pera glabrata (Schott) Poepp. ex Baill.	Peraceae	82.83	X	X
Persea major (Meisn.) L.E.Kopp ●	Lauraceae	23.05	X	X
Persea willdenovii Kosterm.	Lauraceae	23.05	X	X
Pimenta pseudocaryophyllus (Gomes) Landrum	Myrtaceae	30.93	X	X
Piptocarpha axillaris (Less.) Baker ●	Asteraceae	27.36	X	X
Piptocarpha macropoda (DC.) Baker ●	Asteraceae	27.36	X	X
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	34.79	X	X
Protium spruceanum (Benth.) Engl.	Burseraceae	34.79	X	X
Protium widgrenii Engl. ●	Burseraceae	34.79	X	X

Table 2 Continued

Prunus myrtifolia (L.) Urb.	Rosaceae	106.00	X	X
Psidium rufum Mart. ex DC.	Myrtaceae	33.65	X	X
Psychotria nuda (Cham. *et* Schltdl.) Wawra ●	Rubiaceae	30.47	X	X
Psychotria vellosiana Benth.	Rubiaceae	30.47	X	X
Qualea cryptantha (Spreng.) Warm. ●	Vochysiaceae	47.32	X	X
Annona sylvatica A.St.-Hil.	Annonaceae	46.98	X	X
Roupala rhombifolia Mart. ex Meisn.	Proteaceae	44.46	X	X
Rudgea jasminoides (Cham.) Müll.Arg.	Rubiaceae	31.10	X	X
Rudgea triflora Benth.	Rubiaceae	31.10	X	X
Sapium glandulosum (L.) Morong ●	Euphorbiaceae	48.02	X	X
Sapium haematospermum Müll.Arg. ●	Euphorbiaceae	48.02	X	X
Schefflera calva (Cham.) Frodin *et* Fiaschi	Araliaceae	57.42	X	X
Senna velutina (Vogel) H.S.Irwin *et* Barneby	Fabaceae	68.13	X	X
Siphoneugena densiflora O.Berg	Myrtaceae	NA	X	X
Siphoneugena reitzii D.Legrand ●	Myrtaceae	NA	X	X
Siphoneugena crassifolia (DC.) Proença *et* Sobral	Myrtaceae	NA	X	X
Sloanea hirsuta (Schott) Planch. ex Benth.	Elaeocarpaceae	100.40	X	X
Solanum bullatum Vell.	Solanaceae	31.03	X	X
Solanum caavurana Vell.	Solanaceae	31.03	X	X
Solanum leucodendron Sendtn. ●	Solanaceae	31.03	X	X
Solanum pseudoquina A.St.-Hil.	Solanaceae	31.03	X	X
Sorocea bonplandii (Baill.) W.C.Burger *et al.*	Moraceae	77.84	X	X
Symplocos celastrinea Mart. ●	Symplocaceae	42.90	X	X
Symplocos insignis Brand	Symplocaceae	51.55	X	X
Symplocos pubescens Klotzsch ex Benth.	Symplocaceae	42.90	X	X
Tachigali rugosa (Mart. ex Benth.) Zarucchi *et* Pipoly ●	Fabaceae	65.65	X	X
Tapirira guianensis Aubl.	Anacardiaceae	63.98	X	X
Ternstroemia brasiliensis Cambess.	Pentaphylacaceae	103.40	X	X
Toulicia subsquamulata Radlk.	Sapindaceae	NA	X	X
Trichilia casaretti C.DC.	Meliaceae	49.47	X	X
Trichilia catigua A.Juss.	Meliaceae	49.47	X	X
Vantanea compacta (Schnizl.) Cuatrec.	Humiriaceae	106.60	X	X
Vernonanthura discolor (Spreng.) H.Rob. ●	Asteraceae	27.21	X	X
Vernonanthura divaricata (Spreng.) H.Rob. ●	Asteraceae	27.21	X	X
Vismia guianensis (Aubl.) Choisy	Hypericaceae	60.22	X	X
Vismia magnoliifolia Cham. *et* Schltdl.	Hypericaceae	60.22	X	X
Vitex megapotamica (Spreng.) Moldenke	Lamiaceae	57.86	X	X
Vochysia magnifica Warm. ●	Vochysiaceae	34.91	X	X
Vochysia riedeliana Stafleu	Vochysiaceae	34.91	X	X
Vochysia tucanorum Mart.	Vochysiaceae	34.91	X	X
Zanthoxylum fagara (L.) Sarg.	Rutaceae	74.24	X	

distinctiveness of the studied community became more related to the taxonomic groups recorded in the second inventory. Phylogenetic diversity metrics, wood density CWM and AGWB did not show significant relationships with any of the explanatory variables (table 3).

Shifts in wood density CWM were negatively related to shifts in standardized phylogenetic diversity (sesMPD), while both sprouting CWM variables shifted as a function of community composition. Changes in CWM of sprouting intensity were also negatively and significantly related to shifts in standardized phylogenetic diversity and mortality rate. Changes in maximum diameter CWM were positively and significantly related to soil (PC2) and recruitment rate, whereas changes in evolutionary distinctiveness CWM were positively explained by mortality rate. Productivity was positively explained by AGWB of survivors and negatively explained by AGWB of dead individuals, with the latter displaying more important effects than those produced by survivors' AGWB (figure S2-S5; table S1).

DISCUSSION

The ability to monitor changes in biodiversity is critical to species conservation and ecosystem management. While emerging technologies increase the breadth and scope of

Table 3. Results of the analysis of functional composition temporal variations in relation to the evaluated drivers. The first two columns correspond to the analysis of the existing differences between the inventory years through LMM, with the first one (Between years) giving information on the existence of significant differences through the p-value, and the second presenting the tendency of the variables that varied significantly by the "estimate" value provided by LMM. The third corresponds to an analysis of the variation in the functional composition values (Δ CWM) by LMM, with the first presenting the significant explanatory factors and the second (fourth) presenting the estimate values provided by the analysis. * Significant *P*.

Resultados del análisis de las variaciones temporales de la composición funcional en relación con los controladores evaluados. Las primeras dos columnas corresponden al análisis de las diferencias existentes entre los años de inventario a través del GLMM, la primera (entre años) brinda información sobre la existencia de diferencias significativas a través del valor p, y la segunda presenta la tendencia de las variables que variaron significativamente por el valor "estimado" proporcionado por el GLMM. El tercero y el cuarto corresponden a un análisis de la variación en los valores de composición funcional (Δ CWM) por GLM, el primero presenta los factores explicativos significativos y el segundo (cuarto) presenta los valores estimados proporcionados por el análisis.

Response	Main driver (s)	Estimate
DCA axis 1	Year 2	-0.05*
CWM WD	none	
CWM Spr Freq	Year 2, DCA axis 1	-0.52**; -1.3***
CWM Sprouting	Year 2, DCA axis 1	-0.81**; -1.9***
CWM Max DBH	PC2, PC2:Year 2	-23***; 13.5**
CWM ED	Year 2:DCA axis 1	1.65*
sesPD	none	
sesMPD	none	
sesMNTD	none	
AGWB	none	
Δ CWM WD	Δ sesMPD	-0.86**
Δ CWM Spr Freq	Δ DCA axis 1 (squared)	-9.03*
Δ CWM Sprouting	Δ DCA axis 1 (squared), Δ sesMPD, mortality rate	-8*; -7*; -8.3*
Δ CWM Max DBH	PC2, recruitment rate	3.5**; 3.7**
Δ CWM ED	mortality rate	4.25**
Δ AGWB	Δ AGWB mortality, Δ AGWB survivals	-1.5***; 0.6***

Note: CWM: Community Weighted Means, Δ: temporal variation, WD: Wood Density (g/cm³), Spr Freq: Sprouting Frequency (%), Spr Int: Sprouting Intensity, Max DBH: Maximum Diameter at the Breast Height (cm), ED: Evolutionary Distinctiveness, sesPD: Standardized effect size of Phylogenetic diversity, sesMPD: Standardized effect size of mean pairwise distance, sesMNTD: Standardized effect size of mean nearest neighbor distance, Δ: delta - difference from first to second year.

Nota: CWM: Medios ponderados de la comunidad; Δ: variación temporal; WD: Densidad de madera (g cm⁻³); Frecuencia Spr: Frecuencia de brotación (%); Spr Int: Intensidad de brote; DBH máx .: diámetro máximo a la altura del seno (cm); ED: distinción evolutiva; sesPD: tamaño del efecto estandarizado de la diversidad filogenética; sesMPD: tamaño del efecto estandarizado de la distancia media por pares; sesMNTD: tamaño del efecto estandarizado de la distancia media más cercana al vecino; Δ: delta - diferencia de primer a segundo año.

data acquisition, monitoring efforts are still spatially and temporally fragmented, and taxonomically biased. Small changes or a decline in species abundances can lead to a disruption of a community structure and function (Del Vechio *et al.* 2016). These processes should not be underestimated, as the disappearance of a community can not only occur by the direct elimination of vegetation. Rather, gradual changes in the functional characteristics and species composition of a community may lead to the emergence of a new community in terms of the combination of species and community function (Del Vechio *et al.* 2016).

Some of the strongest and most significant catalysts of ecological processes are climatic variations (Fine 2015). Although we will not discuss whether and to what extent climate variations across the time span covered by our study were from anthropogenic origin, we raise the possibility of the recorded changes in community aspects (figures 2 and 4) being catalyzed by rainfall variation.

Concerning the changes in floristic composition (table 2), mortality was recorded for 60 species whereas recruitment was recorded for 39 species. Within these mortality- and recruitment-related groups of species, eight species disappeared from the community while three were included. Accordingly, even if local extinction is balanced by immigration, extinction is not random with regard to identity and functional performance, hence changing composition will have important consequences for ecosystem functioning (Hillebrand *et al.* 2017).

We also recorded structural changes, which could be verified through the significant relationship between CWM of maximum diameter and soil texture (PC2), in which the changes in the effect of soil over the vegetation between the inventory years are reaffirmed by variation in CWM of maximum diameter. Communities in sandy soils had a higher reduction in DBH - less water availability contributing to the death of large individuals. Soil texture is an important driver of community structure, influencing species tolerances to habitat conditions (Maia *et al.* 2020). The different responses displayed by the plants to the same environmental variables through the studied period indicate that precipitation fluctuations in the timeframe of this study likely affected the relationship between plants and soil resources by decreasing water availability (Maia *et al.* 2020), demonstrated mainly through the high mortality of large individuals (in terms of DBH).

Still concerning the structural changes, the sample units with highest recruitment rates displayed a decrease in CWM of maximum diameter. A few studies have shown that, when recruitment is high, competition for resources among the individuals coinhabiting the community increases, due to less investment in radial growth (Ali and Yan 2017).

Our results emphasize that environmental variation in small spatial and temporal scales can potentially yield significant community changes. For instance, between the first and second inventory years, we found that the effect of species composition over the CWM of evolutionary distinctiveness increased. Additionally, mortality had a positive effect over the Δ CWM of evolutionary distinctiveness in the studied timeframe. This seems that the species in the second inventory (year 2017) are more evolutionarily distinct in the context of the entire community than they were in the first inventory, with more species with high ED in the second inventory (Morelli *et al.* 2018). Therefore, the community is in fact becoming more evolutionarily distant in terms of the species that compose it.

Traits that allow the persistence of species in a certain habitat may increase their fitness, enhancing survival capacity and competitive performance (Bond and Midgley 2001). Sprouting ability can be considered one of these fitness-enhancing traits under stressful conditions (*e.g.* flooding: Araújo *et al.* 2017). The number of sprouts, frequency of sprouting and number of sprouting species all decreased in our study area over time. We thus raise the possibility of precipitation oscillations having caused the death of stems, beyond the death of individuals. Furthermore, we found a negative relationship between sprouting variable and net relatedness (sesMPD), showing that the environment is selecting species with low sprouting ability. This is contradictory with other studies which have suggested that disturbance-adapted species should thrive under environmental oscillations (Solar *et al.* 2015).

An important result to be considered is that the AGWB variation in mortality (Δ AGWB mortality) was higher than the variation in survivors (Δ AGWB survivals). This shows that the forest community studied here is losing biomass, which can be partly attributed to the mortality of large trees. For instance, *Tachigali rugosa* had the highest biomass loss and did not recruit any individuals in the second inventory year. Other studies have found links between the mortality of large trees and extreme drought events in the Amazon region, being mainly attributed to the mechanisms of hydraulic failure from embolism (see Phillips *et al.* 2009).

In addition, other causes that may have contributed to the biomass decrease recorded here were changes in wood density. There was an increase in the number of species with low wood density in the sample units where sesMPD values also decreased. The increase in the number of lower wood density species recorded by us suggests that the opening of gaps by the death of large-stemmed individuals likely favored the colonization of fast-growth species (Plas *et al.* 2016). This could mean that: (i) the beginning of the community homogenization process has been recorded, derived from both the increase in the number of colonizing species and the simultaneous death of large trees, moreover (ii) high density wood species are more drought tolerant, therefore, given the predictions of the future scenario in which long periods of drought may occur (Gloor *et al.* 2015), species with low wood density will be the first to be eliminated.

CONCLUSIONS

The search for protection and monitoring of biodiversity is a worldwide concern (including goals to be achieved this year) and studies like ours, about the short term changes of a forest community, not only contribute to a better current understanding of the functioning of forests, but also better capture the possible transformations that the forest community is going through. We verified this through the quantitative changes in the measured parameters (*e.g.* density wood, biomass), qualitative with regard to the taxonomic composition, consequently generating a change in the phylogenetic and functional structure of the community. We were also able to detect a substitution of species with lower wood density, a species disappearance (we highlight the species *Tachigali rugosa*, large-stemmed ones and canopy species). All these changes are seen as indications that the community is taking on a new form, which may cause changes in its functioning. What we want to highlight here is that a monitoring study in a short period may indicate the direction in which the community is moving.

ACKNOWLEDGEMENTS

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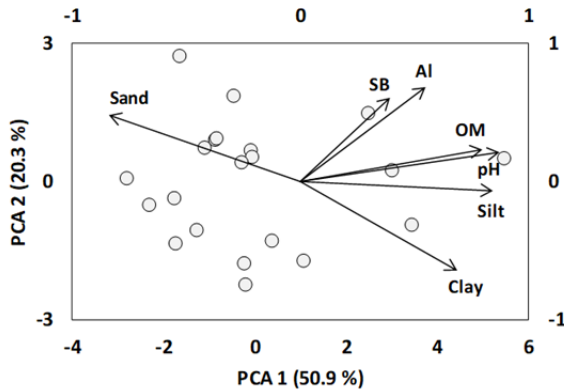## SUPPLEMENTARY MATERIAL

Figure S1. Principal Components Analysis (PCA) for edaphic variables of fertility and texture for the sample units of the Uppermontane Semideciduous Tropical Forest sampled. <u>Note</u>: Al: Aluminum; SB: Sum of Bases; OM: Organic Matter; pH: pH in water; Silt: proportion of Silt; Sand: proportion of Sand; Clay: proportion of Clay.

Análisis de Componentes Principales (PCA) para variables edáficas de fertilidad y textura para las unidades de muestra del Bosque Tropical Semideciduo Uppermontane muestreado. Nota: Al: aluminio; SB: Suma de bases; OM: materia orgánica; pH: pH en agua; Limo: proporción de Limo; Arena: proporción de arena; Arcilla: proporción de arcilla.
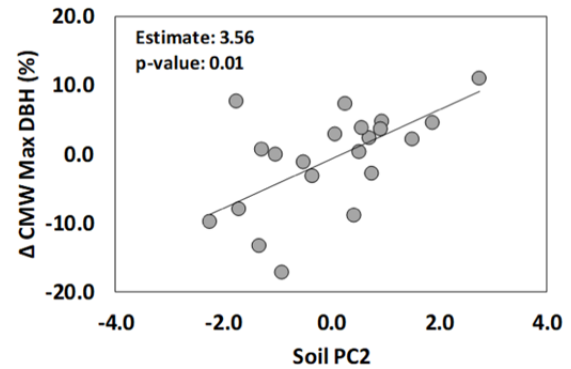

Figure S3. Relation between the Temporal Variation (Δ) of the Maximum Diameter at the Breast Height Community Weighted Means (%) and the Second axis of the Soil Principal Component Analysis (Soil PC2) for the sample units of the Upper montane Semi-deciduous Tropical Forest.

Relación entre la variación temporal (Δ) del diámetro máximo en la media ponderada de la comunidad de la altura del seno (%) y el segundo eje del análisis de componentes principales del suelo (PC2 del suelo) para las unidades de muestra del semi-caducifolio montano superior Bosque tropical.
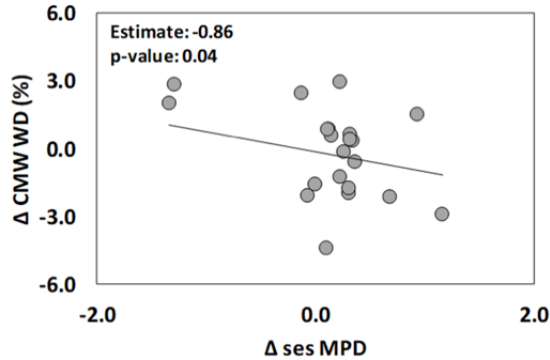

Figure S2. Relation between the Temporal Variation (Δ) of the Wood Density Community Weighted Means (%) and the Standardized effect size of mean pairwise distance (sesMPD) for the sample units of the Upper montane Semi-deciduous Tropical Forest.

Relación entre la variación temporal (Δ) de las medias ponderadas por la comunidad de densidad de madera (%) y el tamaño del efecto estandarizado de la distancia media por pares (sesMPD) para las unidades de muestra del bosque tropical semi-caducifolio montano superior.
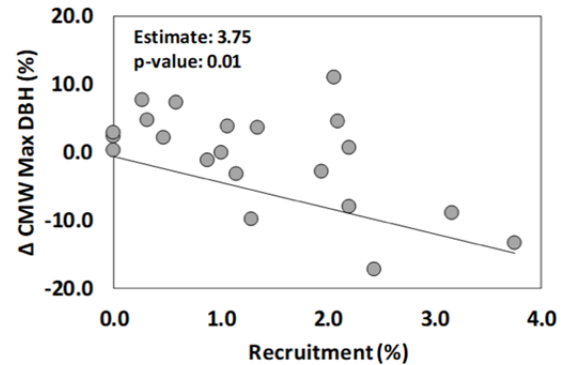

Figure S4. Relation between the Temporal Variation (Δ) of the Maximum Diameter at the Breast Height Community Weighted Means (%) and the Recruitment Rate for the sample units of the Upper montane Semi-deciduous Tropical Forest.
Relación entre la variación temporal (Δ) del diámetro máximo en la media ponderada comunitaria de la altura del seno (%) y la tasa de reclutamiento para las unidades de muestra del bosque tropical semi-deciduo montano superior.
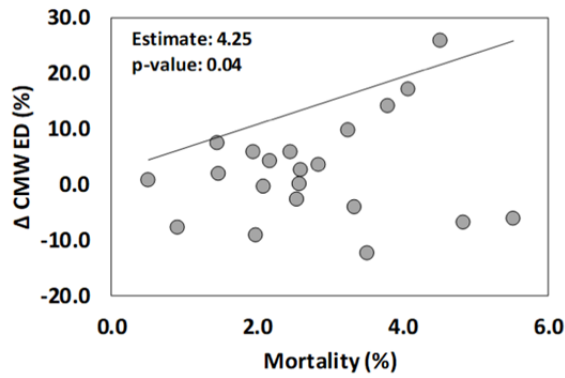
Figure S5. Relation between the Temporal Variation (Δ) of the Evolutionary Distinctiveness Community Weighted Means (%) and the Mortality Rate for the sample units of the Upper montane Semi-deciduous Tropical Forest.

Relación entre la variación temporal (Δ) de las medias ponderadas por la comunidad de distinción evolutiva (%) y la tasa de mortalidad para las unidades de muestra del bosque tropical semi-caducifolio montano superior.

Table S1. Balance of ΔAGB for the two inventories of the seven species with the highest VI.

Balance de ΔAGB para los dos inventarios de las siete especies con el VI más alto.

Year 1			Year 2		
Species	AGB	ΔAGBmort	Species	AGB	ΔAGBmort
Rudgeajasminoides	13.14458	0.3137912	*Rudgeajasminoides*	11.22698	0.002443
Tachigali rugosa	46.84067	1.8886353	*Alchorneatriplinervia*	23.07527	0.005138
Alchorneatriplinervia	21.69688	0.372533	*Tachigali rugosa*	39.1154	0
Solanum leucodendron	4.15601	0.4826296	*Rudgeatriflora*	2.107696	0.000583
Rudgeatriflora	1.918495	0.0056534	*Amaioua intermedia*	5.053149	0.002291
Guatteriavillosissima	6.484367	0.1229875	*Solanum leucodendron*	0.956283	0
Siphoneugenadensiflora	5.659164	0.0255838	*Siphoneugenadensiflora*	6.194287	0.001721