Climate change and forest dynamics: three decades of monitoring

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Abstract

It is well appreciated that moist tropical forests from South America have been broadly affected by climate change. However, long-term trends of seasonal forests are still largely understudied. Here, we evaluate the long-term ecological trends of seasonal Brazilian forests. We used 33 years of locally collected soil and vegetation data (837 tree species) gathered from 34 hectares of evergreen, semideciduous and deciduous forests. We expected them to be more sensitive than resilient to climate change. Across the study region, more species were extinct (315) than locally recruited (238). Locally extinct species' niches were characterized by lower temperatures and higher precipitation. Climatic variables were the main drivers of productivity decrease, especially for larger trees. Deciduous forests were the most vulnerable for being at their ecological threshold. For encompassing a broad temporal scale, our study provided a detailed view of species responses and ecosystem function in tropical forests.

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STATEMENT OF AUTHORSHIP

R Santos and M Fontes planned and designed the research, and conducted fieldwork. G de Paula, F Araujo, N Fagundes, P Coelho, J Morel, A Santos, G Menino, C Souza and N Aguiar-Campos conducted fieldwork. G de Paula, V Maia, C Farrapo, C Souza analysed data. G de Paula, V Maia and N Aguiar-Campos wrote the manuscript.

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DATA ACCESSIBILITY STATEMENT

We declare that should the manuscript is accepted, the data supporting the results will be filed in an appropriate public repository (Dryad, Figshare or Hal) and the DOI data included at the end of the article.

ABSTRACT

It is well appreciated that moist tropical forests from South America have been broadly affected by climate change. However, long-term trends of seasonal forests are still largely understudied. Here, we evaluate the long-term ecological trends of seasonal Brazilian forests. We used 33 years of locally collected soil and vegetation data (837 tree species) gathered from 34 hectares of evergreen, semideciduous and deciduous forests. We expected them to be more sensitive than resilient to climate change. Across the study region, more species were extinct (315) than locally recruited (238). Locally extinct species' niches were characterized by lower temperatures and higher precipitation. Climatic variables were the main drivers of productivity decrease, especially for larger trees. Deciduous forests were the most vulnerable for being at their ecological threshold. For encompassing a broad temporal scale, our study provided a detailed view of species responses and ecosystem function in tropical forests.

INTRODUCTION

Tropical forests harbour the highest portions of global biodiversity, endemism, terrestrial carbon stocks and carbon flux (Pan et al. 2011; Esquivel-Muelbert et al. 2019). However, current changes in the global climate have been profoundly altering tropical forest ecosystem processes, dynamics, diversity and productivity (Esquivel-Muelbert et al. 2018; McDowell et al 2018; Janssen et al. 2020; Sentinella et al. 2020; Sullivan et al. 2020). In this context, the naturally drought-exposed seasonal forests, on the climatic threshold to sustain forest vegetation, may be the most affected by climate change (Allen et al. 2017; McDowell et al 2018). In this context, the naturally drought-exposed seasonal forests, which are already on the threshold of suitable forest-supporting climate, may be the most affected by climate change.

Changes in the amount and distribution of rainfall, coupled with rising temperatures and rising atmospheric CO_2, have contributed to reduce overall tropical forest biomass, mostly through rising tree mortality (Lewis et al. 2004; Allen et al. 2017; McDowell et al. 2018; Hubau et al. 2020). The higher temperatures provoked by high atmospheric CO_2 increase respiration rates, transpiration and lead to carbon deficits and water loss (McDowell et al. 2018; Hubau et al. 2020). Shifts in rainfall distribution may add up to the stress already endured by trees under unfavourable conditions, such as advanced age and precarious local conditions. Additional damage may be inflicted by insects and pests in the stems and roots, causing these weakened trees to succumb to death (Allen et al. 2010). In other cases, water deficit may lead to hydraulic failure through drought-induced cavitation and embolism; or its effects may be reflected in carbon deficits that limit metabolic activity (McDowell et al 2018).

Species responses to climate change may differ based on their tolerances to environmental change (De Laender et al. 2016; Esquivel-Muelbert et al. 2019; Doudová & Douda 2020). As a consequence, forests have become more sensitive and closer to their survival thresholds under climate change (Allen et al. 2017; Phillips 2019; Janssen et al 2020; Sentinella et al. 2020). In this scenario, the demographic balance between mortality and recruitment have significantly differed across species, which is not only translated into taxonomic composition dynamics, but also changes in niche and ecosystem function (Esquivel-Muelbert et al. 2018; Pinho et al. 2019; Doudová & Douda 2020).

Although recent studies have identified increased vulnerability of moist tropical forests to climate change (Esquivel-Muelbert et al. 2018; Esquivel-Muelbert et al 2019; Hubau et al. 2020; Sullivan et al. 2020), it is still uncertain how seasonal tropical forests may respond, given their already low precipitation and high temperature conditions. Recent evidence has been found of seasonal tropical forest vulnerability to changes in drought intensity, frequency and length (Allen et al. 2017; Castanho et al. 2020; Janssen et al. 2020). To better understand the responses of these forests to climate change, more studies are needed that encompass larger timeframes, which allow to identify the effects of slow-changing variables on forest dynamics. However,

data of this nature are difficult to obtain for requiring decadal efforts of field data collection. This has left a knowledge gap about the long-term ecological trends of several regions in the world, and in the tropical part of South America, it is especially true for extra-Amazonian seasonal tropical forests.

Here, we use long-term monitoring data of 30 forest sites in southeast Brazil, aiming to identify the temporal trends, environmental effects and intrinsic characteristics of 837 tree species. Our data encompass broad climatic space and three forest types: deciduous, semideciduous and evergreen. This dataset allows us to investigate micro (soil and species attributes) and macro (climate) ecological interactions through time. We hypothesised that seasonal forests are sensitive to and shaped by climate change. We were able to assess this hypothesis by closely monitoring all tree species in the dataset with a forest dynamics approach. To this end, our study sought to identify: (i) whether there are differences in the number of locally recruited and locally extinct species and how this difference varies through time; (ii) which environmental variables influence the number of recruited and extinct species; (iii) if a species' tendency to local recruitment or local extinction is influenced by its climatic niche; and (iv) which environmental variables and species attributes influence the productivity of forest species populations?

METHODS

Study sites

This study was conducted in 30 permanently monitored forest sites located in southeast Brazil (Figure 1). The largest distances among sites are of 900 km (latitude) and 177 km (longitude). Altitudes vary between 447 and 1490 meters above sea level, whereas mean annual precipitation (MAP) varies between 763 and 1831 mm, and mean annual temperature (MAT) between 17.1 and 25.4 °C. The data include three forest types distinguished by deciduousness and climate (details in Supplementary Material Table S1): (i) five evergreen forest sites, with little to insignificant deciduousness and under the coldest and wettest climate in the dataset (measured between 1995-2019); (ii) sixteen semideciduous forest sites, with 20-50% of canopy deciduousness during the dry season and under an intermediate climate in the dataset (measured between 1987-2019); (iii) and nine deciduous forest sites, with more than 50% canopy deciduousness during the dry season and under the driest and hottest climate of our dataset (measured between 2002-2019). All sites are closed-canopy and mixed-age forests with similar conservation statuses, with no indication of wood extraction or fire occurrence.

Vegetation data were collected from 400 m² plots, distributed across each site aiming to capture local heterogeneity reliably (total of 34 hectares sampled). Each site was measured at least twice, with an inclusion criterion equal to or higher than 5 cm of quadratic mean diameter at the reference height (1.30 m; dbh). All individuals that met the inclusion criterion were tagged and their point of measurement (POM) recorded. We used the POM as a reference for the subsequent measurements. When the POM of a given stem needed to change between measurements, we estimated stem diameter growth from the ratio between the current and previous POMs (Talbot, et al. 2014). Tree identification was performed by specialists in the field or by consulting herbaria. Species names followed APG IV (Angiosperm Phylogeny Group, 2016) and were standardised based on The Plant List (2020).

We extracted wood density values of all individuals from the global wood density database (Chave et al., 2009; Zanne et al. 2009). When wood density was not available at the species level, we used the average wood density value of other species within the same genus or family. We calculated each tree's aboveground woody biomass (AGWB) with the pantropical allometric equation proposed by Chave et al. (2014), with package *biomass* (Réjou-Méchain, Tanguy, Piponiot, Chave, & Hérault, 2017) in the R environment. We used the modified version of this equation because information on tree height was unavailable. We corrected the values of AGWB productivity with the CIC1 equation by Talbot et al. (2014). We removed the productivity of recruited species because individual AGWB is non-numeric. We calculated the average AGWB (or average size) of each population based on their initial total biomass (sum of AGWB of all individuals) divided by the total number of individuals at the beginning of monitoring.

We considered as "locally extinct" those species which disappeared from their original occurrence area, in one or more sites; as "regionally extinct" those species which disappeared in all sites of our dataset; and as

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"recruited" those species which were absent from all areas in the first measurement, but met the inclusion criterion at a certain point and remained in the dataset until the last measurement.

Atmospheric CO₂ concentration

We used annual mean values of atmospheric CO_2concentration (ppm) from the Mauna Loa record (NOAA, 2020; www.esrl.noaa.gov/gmd/ccgg/trends/weekly.html accessed March 17, 2020). We used in the models the CO_2 value corresponding to the mid-point of each census interval. Note that atmospheric CO_2 concentration (CO_2) is strongly correlated with year (r = 0.99) (Figure S1).

Climate data

We obtained monthly mean temperature (^{o}C) and monthly precipitation (mm) from the Climatic Research Unit (CRU TS version 4.03; ~3,025-km^2 resolution; released 15 May 2019; https://crudata.uea.ac.uk/cru/data/hrg/) (Harris et al., 2014). Using data from WorldClim 2.1 (Fick and Hijmans, 2017), we downscaled the CRU data to 1 km^2 and then applied the monthly correction for all months in each census interval. We used the delta spatial downscaling method, see Peng et al., (2019) for details. The average values of MAT and MAP of the years within each census interval were used in the analyses. For the census intervals that ended in 2019, to which climate data were not available in CRU TS version 4.03, we used climate data ranging from the start of the interval to the end of 2018. To estimate the species climatic niches, we opted to use the bioclimatic variables from WorldClim 2.1 for being a long-term synthesis of the sites' climate.

Soil data

In the first inventory of each site, soil surface samples (20 cm of depth) were collected in each plot. Following the protocol by the*Empresa Brasileira de Pesquisa Agropecuária* (EMBRAPA, 1997) the following soil attributes were obtained: pH in water (pH), phosphorus (mg/cm^3) (P), potassium (mg/cm^3) (K), calcium (cmol/dm^3) (Ca), magnesium (cmol/dm^3) (Mg), aluminum (cmol/dm^3) (Al), soil organic matter (dag/kg) (SOM), sand percentage (dag/kg) (sand %), silt percentage (dag/kg) (silt %) and clay percentage (dag/kg) (clay %). We calculated the means of each soil variable for each site. Hereafter, sand % will be used as a proxy for soil texture.

Data analysis

All analyses were carried out in the R environment version 3.6.1 (R Core Team 2019) and graphics were obtained through the packages*ggplot2* , *jtools* and *interactions* (Wickham, 2016; Long, 2019b, 2019a). Species climatic niches were estimated from the weighted average values of mean annual temperature (bio 1) and annual precipitation (bio 12) of all sites where each species was recorded. Weights were based on the average AGWB of the species in each site across all census intervals. We opted to weigh the species' niches with their AGWB rather than abundance because by better synthesizing the species' responses to local conditions. We ran the analysis for each forest type separately because climate is strongly correlated with forest type. This approach prevented us from including climate and forest type in the same models, avoiding high variance inflation factors (VIF > 4).

Balance between recruitment and extinction

We tested if the number of extinct and recruited species differed significantly from each other, and estimated the temporal trend of each group (i.e., the interaction between extinct/recruited and year). For this, we used generalized linear mixed effects models (GLMM) using Poisson family. Because observations were nested within sites and within census intervals, we accounted for the random effects of site and census interval. We used the natural logarithm of the multiplication between site sampled area and census interval length as an offset variable to control for their effects on the species count.

*count of species ~ status*year* (eqn 1)

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Equation 1 describes the global model of extinction/recruitment balance with all variables included in the R notation. Interaction effects are represented by "*".

Environmental drivers of tree extinction and recruitment

The effects of climate and soil on the number of recruited and extinct species were estimated using GLMM, including site as a random effect. We used Poisson family and included the natural logarithm of the multiplication between site sampled area and census interval length as an offset variable to control for their effects on the species count.

y ~ MAP+MAT+Year +pH+P+K+Ca+Mg+Al+SOM+sand% (eqn 2)

Equation 2 describes the global model of the effects of environmental variables on the number of extinct and recruited species, with all variables included in the R notation. Note that y is the number of extinct and number of recruited species.

Climatic niche

Niche differences (bio 1 and bio 12) between extinct and recruited species were tested using linear mixed effects models (LMM). As response variables, we used the mean niche value of the species that were either extinct or recruited in each census interval. We also estimated the temporal trends of the extinct and recruited species' niches by including the interaction between status and year in the models. Because observations were nested within sites and within census intervals, we accounted for the random effects of site and census interval.

*y ~ status*year* (eqn 3)

Equation 3 describes the global niche model with all variables included in the R notation. Interaction effects are represented by "*". Note that y is the mean values of bio 1 and bio 12, two dimensions of the climatic niches of extinct and recruited species.

Species productivity

We fitted LMM to estimate the influence of biotic (mean individual size, wood density and climatic niche) and abiotic variables (atmospheric CO_2, MAP and MAT) on species AGWB productivity. We included site, census interval, family, genus and species as random effects. We also tested the interactions between environmental variables (CO2, MAP and MAT) and species attributes (mean individual size, wood density and niches) on productivity.

*species productivity ~ (MAP+MAT+ Year) * (mean ind. size + niche bio 1+ niche bio 12) + WD* (eqn 4)

Equation 4 describes the global model of species AGWB net productivity, with all variables included in the R notation. Additive and interaction effects are represented respectively by "+" and "*".

Model assumptions, model selection and other details.

We ensured normality and homoscedasticity of LMM residuals through residuals inspection and checked for overdispersion in GLMMs. In all models, we checked for residual spatial autocorrelation using Moran's I test, implemented in package *ncf* (Bjørnstad, 2018). Random effects were used to deal with the temporal autocorrelation and the data's nested design.

For the balance and niche models, we obtained pairwise comparisons between levels with the package *emmeans* (Lenth et al. 2018). We used the Akaike Information Criterion of second order (AICc) for model selection (Burnham, Anderson, & Huyvaert, 2011). From the global model of each response variable, we obtained the set of best models (ΔAICc [?] 4) (Burnham et al. 2011). To avoid collinearity issues, the selected models were constrained to only contain explanatory variables with r [?] |0.6| (Dormann et al., 2013), ensuring low variance inflation factor (VIF [?] 4). We adopted a multimodel inference approach, by averaging the coefficients of the selected models and using these conditional averaged coefficients as final results (Burnham et al., 2011). The relative importance of the predictor variables was not considered because

some variables were not contained in the same number of models due to collinearity issues, which could bias the sum of Akaike weights (Burnham et al., 2011).

We used packages *lme4* (Bates et al., 2015) to fit the (G)LMMs, *lmerTest* to calculate denominator degrees of freedom and *MuMIn* (Bartón, 2018) for model selection, model averaging and to obtain the marginal R^2 (variance explained by the fixed effects) (Nakagawa & Schielzeth, 2013).

RESULTS

Balance between recruitment and extinction

Throughout the 33 years of monitoring, a total of 837 species belonging to 87 plant families were recorded. 315 species were locally extinct and 28 species were regionally extinct (Table S2), whereas 238 were recruited in at least one site across measurement years. In terms of number and percentage of locally or regionally extinct and recruited species, the highest number was found in semideciduous forests. In semideciduous forests, we also found a significantly higher number of extinct species than recruited ones (Figure 2a). However, the largest gap between the number of extinct and recruited species was found in the deciduous forests (Figure 2b), with a significantly higher number of extinct species. In evergreen forests, although the number of extinct species was higher than the number of recruits, this balance was stable through time (Figure 2c).

Environmental drivers of extinction and recruitment

The recruitment and mortality of species are conditioned by different environmental factors in the different forest types (Table 1). Mean annual precipitation (MAP) was a common driver of mortality in all forest types, with a negative effect on deciduous and evergreen forests. Mean annual temperature (MAT) positively affected species recruitment in deciduous forests and negatively affected species mortality in semideciduous forests. Time (year) was only a significant factor for tree mortality in deciduous forests. Soil characteristics influenced tree mortality and recruitment in all forest types. Recruitment was positively influenced by aluminium in deciduous forests and positively influenced by magnesium in evergreen forests. In semideciduous forests, potassium positively influenced mortality.

Climatic niche

Beyond the differences between the balance in recruited and extinct species, we also found that their climatic niches are significantly different. In the deciduous forests, recruited species niches are characterised by higher temperatures, meaning that those adapted to colder temperatures are being locally excluded and replaced by hotter climate species (Table 2). A similar trend regarding the precipitation niche was found in the deciduous forests: recruited species' niches are negatively associated with low precipitation (Table 2), meaning that species with higher precipitation niches are being recruited. In semideciduous and evergreen forests, no significant differences regarding climatic species niches (temperature and precipitation) were found (Tables 2 and 3).

Species productivity

Interactions between some environmental variables and species attributes significantly affected productivity. Species' attributes reacted differently to the environmental variables, yielding different responses in each forest type (Table 3). In the deciduous forests, MAP and MAT (mediating variables) positively affected productivity, with a stronger effect in species with higher average individual sizes (i.e., higher average of aboveground woody biomass) (Figure 3 c-e). Importantly, precipitation is decreasing over time (Figure S5).

In semideciduous forests, we found a positive effect of MAP and MAT (mediating variables) on productivity (Table 3; Figure 3 f-h). The effects of climate were also stronger on species with higher average individual sizes. Time (year) also influenced productivity, but negatively. Considering the quartile averages, however, productivity increased over time.

Productivity in the evergreen forests was negatively affected by climate (mediating variables) and by time (year) (Figure 6). But these effects were weaker in evergreen than in deciduous and semideciduous forests,

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and stronger in species with lower average size.

The results for all forest types having biomass as a mediating variable can be found in the Supplementary Material.

DISCUSSION

We found a negative balance between mortality and recruitment, with more species being locally extinct and fewer recruited, reflecting that there are more species disappearing than being incorporated into our forests. Niches of locally extinct species were associated with high precipitation and low temperatures, which differed from the niches of recruited species. Climatic niche variables (MAP and MAT) were the main drivers of reduction in species productivity, with stronger effects on species with higher average sizes. Despite variations in these results among forest types, all of them are being affected by changes in climate.

The negative balance in demography found in our study reflects a high number of local extinctions. Other studies have observed an increasing number of extinctions at global and regional scales (Ceballos et al. 2015; Esquivel-Muelbert et al. 2018; Humpreys et al. 2019; Sheldon et al. 2019; Neves et al. 2020). And not only are these losses decreasing species richness, but they may also entail losses of evolutionary groups and ecosystem functions, leading to increasing phylogenetic and functional homogeneity (Aguirre-Gutiérrez et al. 2020). Moreover, structural changes deriving from local species extinction may decrease these ecosystems' capacity to cope with climate changes (Allen et al. 2017).

The climatic variables MAP and MAT significantly affected the demographic parameters, with significant effects of MAP on mortality in all forest types. Reductions in MAP can produce water deficit in ecological systems. As a response, tree communities may display increased mortality from carbon starvation, hydraulic failure and death of already vulnerable trees (Lewis et al. 2004; Allen et al. 2010; McDowell et al. 2018). MAT effects, on the other hand, differed across the forest types, with a positive effect on recruitment in deciduous forests and a positive effect on mortality in semideciduous forests. Deciduous forest species are better adapted to climatic extremes (Santos et al. 2014; Allen et al. 2017); therefore, increases in MAT may promote the recruitment of species adapted to higher temperatures (Santos et al. 2014; Sentinella et al. 2020). In the case of semideciduous forests, which occur under intermediate climate (Oliveira-Filho & Fontes 2000) and whose plant lineages are adapted to a range of tropical temperatures (Neves et al. 2020), some species may be operating near their survival thresholds in terms of temperature. These are likely the first species to succumb under rising temperatures (Sentinella et al. 2020). Moreover, deciduous forests had a positive relationship between mortality and time (year), indicating that they are sensitive to climate change. This trend has also been reported elsewhere (Allen et al. 2017; Castanho et al 2020; Maia et al. 2020; Mendes et al. 2020, Maia et al., in press). Soil effects differed across forest types, with specific nutrients producing different effects on demography. Plant-soil association reflects the species' tolerances to soil conditions and is an important factor for plant community structure (John et al. 2007; Turner et al. 2018; Maia et al. 2019a).

Our results show that deciduous forest composition is undergoing a trend of niche substitution from the occurrence of lower-temperature and higher-precipitation species to higher-temperature and lower-precipitation species. This trend has also been found in other tropical forests, from wet to dry, in response to rising temperatures and increasing water stress (Enquist & Enquist, 2011; Butt et al. 2014; Esquivel-Muelbert et al. 2018; Sentinella et al. 2020). Furthermore, environmental variables can alter species fitness, phenology, physiology and diversity, due to niche differences and temporal niche opportunities, which may promote coexistence and shape temporal community dynamics (Sapijanskas et al. 2014; Allen et al. 2017; Esquivel-Muelbert et al. 2018; McDowell et al. 2018). Although the climatic niches of evergreen and semideciduous forest species did not change considerably through time, one cannot assume that their niches are temporally stable. This pattern may arise from competitive dynamics between gains and losses in the representativity of species' climatic niches (Maia et al. 2019b).

Productivity across all forest types was significantly influenced by MAP and MAT, although with different effects in each. The mediating effects of MAP and MAT on the productivity of deciduous forest species was stronger in those with higher average individual sizes (Figure 3 c-e). The influence of MAP suggests that

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larger individuals are more vulnerable to drought effects. Potential reasons for this influence are that (i) higher vapour pressure deficit coupled with (ii) higher temperatures at the sun-exposed crowns (as these are the highest individuals in the forest canopy) and (iii) water transportation over longer stem lengths may altogether lead to xylem embolism and hydraulic failure in the largest individuals (da Costa et al. 2010; Fisher et al. 2010; Corlett 2016; Meakem et al. 2017; McDowell et al. 2018). The positive relationship between MAT and individual biomass led to a decrease in productivity. This result may owe to the optimal temperature interval, decreasing photosynthesis and decreasing carbon gain (da Costa et al. 2010; Fisher et al. 2010; Corlett 2016; Meakem et al. 2017; McDowell et al. 2018). Unless the plants adapt to higher temperatures by increasing their optimal photosynthetic temperature, additional climate warming may reduce tropical forest productivity and carbon storage (Sheldon 2019).

On the other end of the climate spectrum in the study region, we found a decrease in productivity in populations of evergreen forests (Table 3; Figure 6A and 6B), with a negative effect of MAP and MAT in all forest strata (i.e., irrespective of tree size). In the Amazon forest, decreases in the rate of biomass gain suggest that factors related to temporal climate variation may mitigate productivity gains, even with CO_2 fertilization (Lewis et al. 2004; Sullivan et al. 2020). Higher temperature and lower precipitation may hinder plant growth and carbon storage as a result of turgor loss, suggesting that growth controls total photosynthesis more often than the other way around (Lewis et al. 2004; Körner 2015; McDowell et al. 2018). Reduced productivity may also be attributed to increasing individual mortality (especially of large individuals) due to changes in MAP and MAT. Under water deficit conditions, water transport in the larger trees is challenged by gravity and resistance through the stem, which combined with higher evaporative demand from tree crown exposure, increase water column tension and mortality risk (Bennet et al. 2015). Whatever the causes of reduced growth and rising mortality, observations and experiments have revealed an array of responses to climate change by different species and forest strata within tropical communities (Corlett 2016; Poorter et al. 2017; Esquivel-Muelbert et al. 2018; Esquivel-Muelbert et al. 2019). Moreover, evidence suggests that continuous heating is likely to interfere even further on biomass build-up because tropical plants already function at or near their ideal temperatures (Drake et al. 2015; Sentinella et al. 2020).

In semideciduous forest populations, we found an increase in productivity, with positive effects from MAP and MAT when interacting with the mediating variable, biomass (Table 3; Figure 7A and 7B). These forests occur through a range of topographic and altitudinal conditions that provide microclimatic variations that may favour the occurrence of certain species even if broader climatic oscillations occur (Mau et al. 2018; Sheldon et al. 2019). Besides, semideciduous forests are on the threshold between dry and wet environments and are composed by lineages adapted to both kinds of environments (Neves et al. 2020). Therefore, in their case, changes in MAP and MAT may favour biomass increment in those species adapted to a drier and hotter climate.

Our results pointed to a negative relationship between year and productivity for semideciduous and evergreen forests (Table 3; Figure 6C and 7C). Although measuring the potential effects of CO_2 fertilisation on dynamics was not among our goals, other studies have traced a parallel between temporal increases in CO_2 and forest productivity (IPCC 2018; Hubau et al. 2020; Sullivan et al. 2020; Maia et al., in press). Recent studies on old-growth and intact tropical forests have shown that the effects of ongoing CO_2 fertilisation have been neutralised by climate change effects on tree growth and mortality, which are shaped by internal forest dynamics (Hubau et al. 2020; Sullivan et al. 2020). It is forecasted that the carbon sink of intact tropical forests transforms into a negative budget (i.e., biomass loss higher than biomass gain) sooner than the most pessimistic predictions have anticipated (Hubau et al. 2020). Therefore, the future carbon budget will also depend on the dynamics of seasonal tropical forests, secondary forests and restoration projects (Hubau et al. 2020, Mendes et al. 2020).

Climate change has moved from the realm of predictions into the real life, affecting different types of forests in different ways (Esquivel-Muelbert et al. 2018; McDowell et al. 2018; Sentinella et al. 2020; Hubau et al. 2020). Our results highlight the need to encompass a broad range of climatic regimes to understand and

compare the responses of different forest types to climate change. For instance, although deciduous forests are better adapted to drier conditions, they are at the ecological threshold that sustains high-biomass forest formations (Li et al. 2018; Santos et al. 2014), which renders them susceptible to abrupt climate change (Allen et al. 2017; Castanho et al. 2020). Despite the evidence that these forests are vulnerable, further studies are needed to assess the different impacts they suffer from climate change. Temperature shifts alone are potential intensifiers of drought severity (Salazar et al 2007, Lapola et al 2009), and if precipitation continues to decline, changes in bioclimatic space, biomass and productivity will be even more severe than has been reported (Mendes et al. 2020; McDowell et al. 2018; Hubau et al. 2020).

Climate change has been a catalyst for ecosystem shifts in our naturally ever-changing world. Learning the speed of ecosystem responses deserves great attention, but perhaps more urgent is learning the direction and potential consequences these ecosystem changes will have on biodiversity. Therefore, studies encompassing broad temporal scales, such as ours, are able to monitor species responses and ecosystem function through time. For providing a detailed view of ecosystem responses, they can contribute to foster public policy decision-making and international guidelines on biodiversity conservation.

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Table 1 – Main environmental drivers of species recruitment and extinction, along with their estimates. Columns three and four correspond to the variables that changed over time through the GLMM with significant differences in the p-value. The fifth column shows the trend of variables that varied significantly by the "estimated" value provided by GLMM.

		Response	Main driver (s)	Estimate
Deciduous	$R^2{}_{marginal} = 80\%$	Mortality	Year	0.5968**
		Mortality	MAP	-0.6162**
	$R^2{}_{marginal} = 99\%$	Recruitment	MAT	0.8970**
		Recruitment	Al	0.8313**
Semideciduous	$R^2{}_{marginal} = 52\%$	Mortality	K	0.3430**
		Mortality	MAP	0.1349*
		Mortality	MAT	0.2480**
Evergreen	$R^2{}_{marginal} = 67\%$	Mortality	MAP	-0.2863*
	$R^2{}_{marginal} = 64\%$	Recruitment	Mg	0.39955*

Table 2 – Result of the temperature and precipitation niches of the species over time in the different forest types. This table shows the variables contained in the linear average mixed effects model of each response variable and their conditional estimates, standard errors and p-values. The marginal R^2 (variation explained by the fixed effects) of the global model is also shown for each physiognomy.

Medium Annual Temperature -MAT	Medium Annual Temperature -MAT	Medium Annual Temperature -MAT	Medi
		Predictor	**Estir**
Deciduous	$R^2{}_{marginal} = 34\%$	Recruitment	0.925
		Year	0.352
		Recruitment x Year	-0.317
Semideciduous	$R^2{}_{marginal} = 0.2\%$	Recruitment	-0.046
		Year	-0.010
		Recruitment x Year	-0.128
Evergreen	$R^2{}_{marginal} = 17\%$	Recruitment	0.289
		Year	-0.233
		Recruitment x Year	0.117
Medium Annual Precipitation -MAP	Medium Annual Precipitation -MAP	Medium Annual Precipitation -MAP	Medi
Deciduous	$R^2{}_{marginal} =33\%$	Recruitment	-123.3
		Year	-29.23
		Recruitment x Year	31.95
Semideciduous	$R^2{}_{marginal}= 0.2\%$	Recruitament	-0.661
		Year	1.283
		Recruitment x Year	9.058
Evergreen	$R^2{}_{marginal} = 3\%$	Recruitment	-19.05
		Year	10.61
		Recruitment x Year	1.275

Table 3 - Minimum adequate models to predict productivity.

Productivity

Deciduous $R^2_{\text{marginal}} = 14\%$	Deciduous $R^2_{\text{marginal}} = 14\%$	Deciduous $R^2_{\text{marginal}} = 14\%$	Deciduous R^2
Predictor	Estimate	Standard error	P value
Biomass (Mg ha^{-1})	-0.01	0.007	0.05331
MAP (mm)	0.02	0.006	< 0.001
MAT (°C)	0.01	0.006	0.00784
Biomass:MAP	5.13	0.008	< 0.001
Biomass:MAT	3.84	0.005	< 0.001
niche$_{\text{temp}}$	-	-	ns
niche$_{\text{prec}}$	-	-	ns
MAT: niche$_{\text{temp}}$	-	-	ns
MAT:niche$_{\text{prec}}$	-	-	ns
MAP:niche$_{\text{prec}}$	-	-	ns
WD	-	-	ns
Semideciduous $R^2_{\text{marginal}} = 0.8\%$	Semideciduous $R^2_{\text{marginal}} = 0.8\%$	Semideciduous $R^2_{\text{marginal}} = 0.8\%$	Semideciduou
Predictor	Estimate	Standard error	P value
Biomass (Mg ha^{-1})	0.03	0.002	< 0.001
MAP (mm)	-	-	ns
MAT (°C)	-	-	ns
niche$_{\text{temp}}$	-	-	ns
Year	-0.01	0.0003	< 0.001
Biomass:MAP	0.006	0.002	< 0.001
Biomass:MAT	0.014	0.001	< 0.001
Biomass:Year	-0.003	0.003	< 0.001
MAT:niche$_{\text{temp}}$	-	-	ns
MAP:niche$_{\text{temp}}$	-	-	ns
WD	-	-	ns
Niche$_{\text{prec}}$	-	-	ns
MAT:niche$_{\text{prec}}$	-	-	ns
MAP:niche$_{\text{prec}}$	-	-	ns
Evergreen $R^2_{\text{marginal}} = 0.2\%$	Evergreen $R^2_{\text{marginal}} = 0.2\%$	Evergreen $R^2_{\text{marginal}} = 0.2\%$	Evergreen R^2
Predictor	Estimate	Standard error	P value
Biomass (Mg ha^{-1})	-0.04	0.0035	< 0.001
MAP (mm)	-	-	ns
MAT (°C)	-	-	ns
WD	-	-	ns
Year	-	-	ns
Biomass:MAP	-0.012	0.004	0.002
Biomass:MAT	-0.018	0.003	< 0.001
Biomass:Year	-0.029	0.002	< 0.001
niche$_{\text{prec}}$	-	-	ns
niche$_{\text{temp}}$	-	-	ns
MAT:niche$_{\text{prec}}$	-	-	ns
MAP:niche$_{\text{prec}}$	-	-	ns
MAT:niche$_{\text{temp}}$	-	-	ns
niche$_{\text{prec}}$:Year	-	-	ns
MAP:niche$_{\text{temp}}$	-	-	ns
niche$_{\text{temp}}$:Year	-	-	ns

Note: This table shows the variables contained in the linear mixed effects averaged model of each response variable, and their conditional estimates, standard errors and p-values. The marginal R^2 (variance explained by the fixed effects) of the global model of each response variable is shown. Note that "ns" indicate P value > 0.05 and that the estimates, standard errors and P values of the covariates were omitted when not significant.
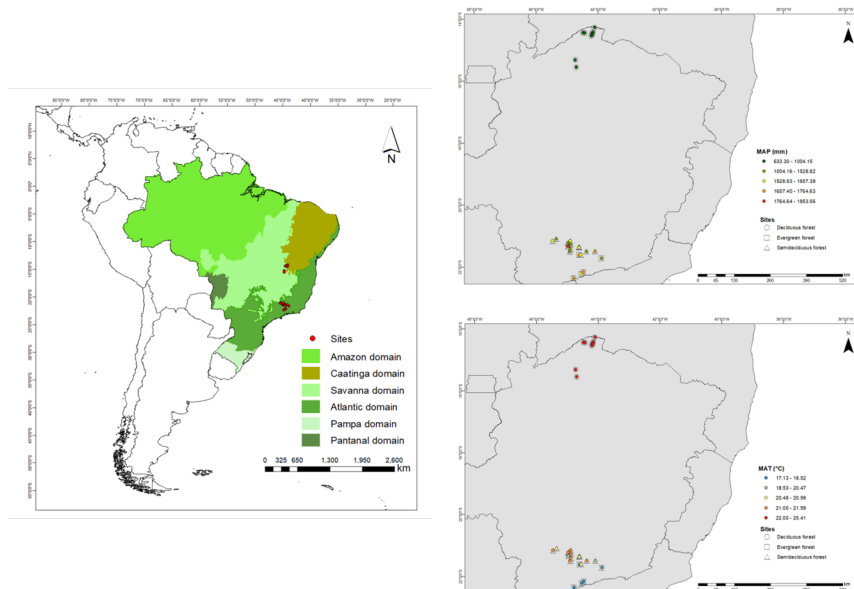

Figure 1. Location of the sampled sites (n = 30) in South America. Note that MAP (mm) is mean annual precipitation and MAT is mean annual temperature, obtained from WorldClim 2.1 (Fick and Hijmans, 2017).
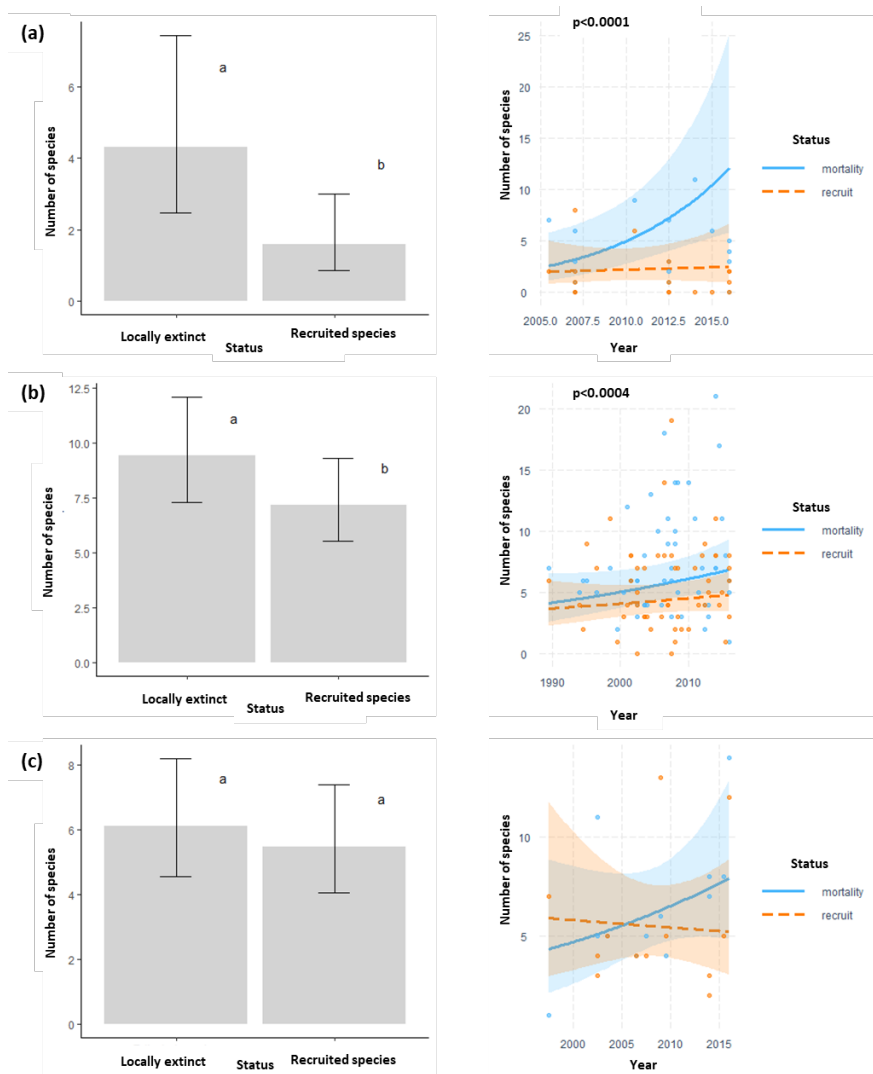
Figure 2 – Difference between locally extinct and recruited species according to the number of species – **(a)** Deciduous;**(b)** Semideciduous; **(c)** Evergreen.
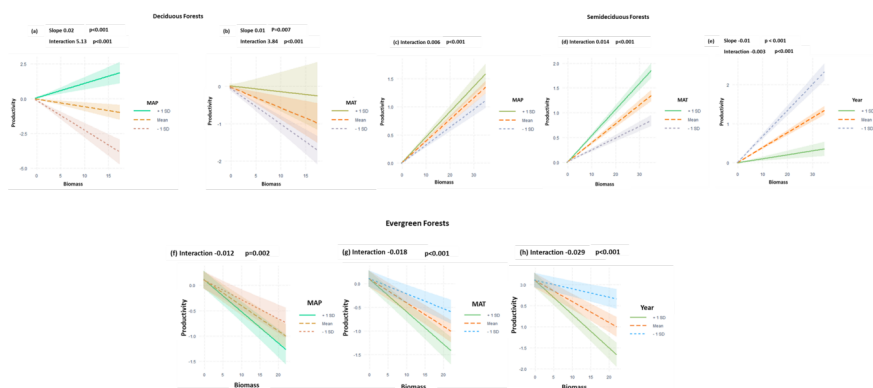
Figure 3 – Variation of productivity (response variable) to the interacting effects of individual biomass (predictor variable) with year, mean annual precipitation (MAP) and mean annual temperature (MAT) (mediator variables). Solid and dashed lines refer to the fitted models with the mean value of the mediator variable more (+) or less (-) its standard deviation. Note that the slope represents the influence of the predictor variable (biomass) in interaction with the mediator variables (MAP, MAT and year) on productivity. **(a-b)** mean annual precipitation (MAP) and mean annual temperature (MAT) in deciduous forests; **(c-e)** mean annual precipitation (MAP), mean annual temperature (MAT) and Year in semideciduous forests; **(f-h)** mean annual precipitation (MAP), mean annual temperature (MAT) and Year in evergreen forests. Shades represent the confidence bands of the fitted lines.