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ORIGINAL ARTICLE

Climatic distribution of tree species in the Atlantic Forest

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Abstract

Species under milder climates (e.g., warm and wet) tend to experience lower variability in temperature and rainfall regimes and might occur in narrower climatic ranges than species that tolerate harsher conditions (e.g., cold or dry climates). Thus, tree species that occur under harsh conditions should have a broader climatic range, being a small subset of the flora. Here, we assess the influence of climate on species distribution of 1138 tree species from the Atlantic Forest biodiversity hotspot. We investigate their range (or niche breadth), and the "center of gravity" index (or niche optima), along with gradients of mean annual temperature and climatic water deficit (CWD). We further identified those species associated with conditions on different ends of temperature and moisture gradients. We found a small subset of species occurring under colder temperatures or under drier conditions, and these species had a wider niche breadth. The warm or wet-affiliated species had narrower ranges along with the temperature and the CWD gradients, respectively. Moreover, species affiliated to warm and those to moister conditions had greater densities near their occurrence limits, thus they may be more susceptible to climate changes. We conclude that global climate changes will affect the incidence and abundance distribution patterns of tree species along this threatened biodiversity hotspot, mainly those with narrow niches and within the limit of its distribution.

Abstract in Portuguese is available with online material

KEYWORDS
biogeography, climate changes, climatic gradients, niche breadth, niche optima, temperature, tolerance, tropical forests, water deficit

1 | INTRODUCTION

A well-known macroecological pattern is that forests in hotter and wetter sites tend to have greater tree species diversity than in colder and drier sites (Gaston, 2000; Myers et al., 2000; Wiens & Donoghue, 2004). This pattern supports the hypothesis that temperature and precipitation regimes are primary drivers of plant species distributions (Baltzer & Davies, 2012; Condit et al., 2013; Jones et al., 2008). Most clades of angiosperms arose in the warm and moist tropics (Wiens & Donoghue, 2004); opposite climatic conditions (e.g., cold or warm and dry conditions) are encountered as stressors for such species, and only a minority may be able to occur in these environments (Currie et al., 2004). Evidence of climate influences on tree richness are found both directly, with more species in warm, moist, and aseasonal climates, and indirectly, with more species in forests with higher stem abundance (Chu et al., 2019). Moreover, species under warm and wet climates in low latitudes typically experience lower variability in temperature and rainfall regimes (Vázquez & Stevens, 2004), and their occurrence may be then restricted to a narrower climatic range. The observation of species distributions across temperature and precipitation gradients (i.e., climatic ranges) can indicate species niche breadth.

The abundance of individual tree species and genera is also correlated with climate variation (Butt et al., 2008; Chu et al., 2019). Along with the climatic range in which a species occurs, a higher number of individuals is expected to be found under the environmental conditions most favorable to that species, and such conditions will then indicate its optimal niche (Chen et al., 2009). Data on abundance, that is, the number of individuals across communities, have been used to quantify the species' optimal niche or the environmental condition in which the species achieves the highest population density (Chen et al., 2009), also called the condition a species is affiliated to (Esquivel-Muelbert et al., 2017). The optimal niche may be independent of the center of the distribution, or range center, as the environment may not always be evenly distributed. A relationship between species abundance and range center arises from the assumption that the environment tends to be more suitable for a given species at the center of the range than near its limits, thus allowing for higher local abundance (Brown, 1984; Holt et al., 1997; McGill & Collins, 2003; Vela Díaz et al., 2020). However, the literature found controversial empirical support for this hypothesis (Abeli et al., 2014; Dallas et al., 2017; Sporbert et al., 2020), which can be due to the influence of biotic interactions or past climate on local abundances (Araújo et al., 2002; Dallas & Hastings, 2018; Sporbert et al., 2020). Thus, the optimal niche shows where species achieve higher performance (local abundance), considering climatically and ecologically more suitable areas. An analysis combining observed optimal niche with range center can highlight whether the higher abundances of species are different from the center of the range, this difference would indicate susceptibility to climate change.

Very low/high temperatures and water deficit are physiologically challenging to plants, making only species with specific ecological strategies able to tolerate them. To withstand cold stress, plants should have traits to avoid being killed by freezing. Cold acclimation integrates a set of physiological and biochemical regulatory events (essentially photosynthesis and respiration) by which plants acquire increased freezing tolerance (Ding et al., 2019). Plant tolerance to heat also involves biochemical adaptations, such as in the membranes' lipid composition and increased production of heat shock proteins (Zhu et al., 2018); however, these strategies are costly and rare in nature. In addition, recent evidence based on species occurrence suggests that many tropical tree species are close to their thermal optima, and even small temperature increases might have negative effects on these species and their communities (Sentinella et al., 2020). Water stress is another critical challenge for plant growth, survival, and dispersal. Sustained periods of severe loss of hydraulic conductivity, for example, are strongly related to tree mortality (Anderegg et al., 2019; Engelbrecht et al., 2007; McDowell et al., 2018; Rowland et al., 2015). Within the tropics, only a small subset of species can cope with water-stress conditions (Esquivel-Muelbert et al., 2016; Krishnadas et al., 2021) by presenting adaptations such as cell survival at low water potentials, deeper root systems, and early stomatal closure (Baltzer et al., 2008; Chitra-Tarak et al., 2021; Pivovaroff et al., 2021). Thus considering that climatic tolerances of species drive species richness patterns along warm-cold or moist-dry gradients, we expect that species occurring at the environmental limits of the gradients (e.g., under low temperatures and/or dry conditions) within a biome to be a small subset of the regional species pool. Considering moist tropical/subtropical regions, these species that can tolerate cold or dry conditions should have wider ranges than those restricted to the less challenging warm and/or wet environments.

Alternatively, harsh climatic conditions may constrain the occurrence of most species (Condit et al., 2013; Saiter et al., 2016) and favor the stress-tolerant species (Pierce et al., 2013). A different flora set is thus expected toward more extreme conditions from moist/warm to dry/hot. In such scenarios, because species adapt different strategies (i.e., investing tolerance to harsh conditions vs. competitive ability under favorable conditions), they would replace each other along environmental gradients, resulting in a substantial species turnover across communities (Leibold & Mikkelson, 2002). The turnover is less evident when multiple environmental variables, varying independently, act simultaneously on species selection (Dambros et al., 2020). Besides turnover, species incidences along gradients can show a nested structure, considering the proportion in which a given species occurs throughout the entire data set (Ulrich & Almeida-Neto, 2012). In a macroecological context, causes of nested structure can be associated with colonization trajectories or selective environmental tolerances among stress gradients, for example. Any pattern of nestedness is specific to the gradient of interest and, if present, it is necessarily associated with differences in species richness and/or species incidence (Almeida-Neto & Ulrich, 2011; Ulrich & Almeida-Neto, 2012).

Here, we use an extensive data set of community inventories from the Atlantic Forest biodiversity hotspot to evaluate how the occurrence and abundance of tree species vary across two main factors that structure the tree species distribution: temperature and water-stress gradients. Previous studies have assessed the primary relevance of water deficit to tree species distribution and abundance in the warm tropical Amazon region (Esquivel-Muelbert et al., 2016). Concerning the Atlantic Forest region, cold temperature conditions can be as important as water deficit in determining tree species distribution, but there are no studies evaluating the influence of temperature across such a broad region and considering community abundance data. In this study, we aim to quantify the niche breadth and the niche optima of 1138 tree species assessing how temperature and water deficit influences species distribution across the Brazilian Atlantic Forest—the second-largest rain/moist forest region of Neotropics expanding between tropical and subtropical latitudes under broad climate gradients (Oliveira-Filho & Fontes, 2000). Particularly, we aim to (i) evaluate the occurrence range of tree species across temperature and water deficit gradients and their relationship to species tolerance limits (upper and lower limits of occurrence); (ii) analyze whether species that tolerate colder and drier conditions are a small subset of species with broader climatic range (nested pattern); (iii) investigate if niche optima are related to the center of the range of each species environmental occurrence (i.e., an expected value to the niche optima); and (iv) test if species affiliated to cold/hot and dry/wet conditions present smaller or broader niche breadths. We finally discuss our results in light of the projections of climate change for the next decades.

2 | METHODS

2.1 | Study area and tree phytosociological data

The Atlantic Forest extends across Brazil's eastern coast and reaches more continental areas in northeastern Argentina and southeastern Paraguay (5–33° S latitude and 35–57° W longitude; Figure 1). The Atlantic Forest has strong gradients of rainfall (annual means varying between 500 and 3000 mm) and temperature (annual means between 10 and 25 °C), which is attributed to its large variation in terms of forest structure, species richness, and composition (Oliveira-Filho et al., 2006), with high alpha and beta diversities of tree species (Bergamin et al., 2017), as well as high tree endemism levels (Lima et al., 2020).

The Atlantic Forest flora has complex origins. Their forests are separated from the Amazonian forests by a corridor of seasonally dry forests and savannas of the semiarid Caatinga (northeastern Brazil), the Cerrado (central Brazil), and the Chaco in Paraguay, Argentina, and Bolivia (Prado & Gibbs, 1993). An abrupt transition to the semiarid Caatinga occurs in northeastern Brazil, where a strip of coastal rainforests is bordered by a narrow belt of seasonal semi-deciduous forests. The coastal rain and moist forest transition with Cerrado involves a much larger extent of semi-deciduous forests in southeastern Brazil that becomes increasingly wider toward the south and integrates a complex mosaic with savannas. In the subtropical region, where frost is frequent in the winter, large areas of Araucaria Forest in the plateaus separate the moist coastal forests and the western semi-deciduous forests (Oliveira Filho & Fontes, 2000). The current phytogeographic pattern along the Atlantic Forest is also a consequence of past climatic fluctuations (Carnaval et al., 2014; Werneck, 2011) that led to the expansion and retraction of distinct vegetation types (Behling, 1997; Costa et al., 2018). During the Last Glacial Maximum, a large stable area of the Atlantic Domain in the north (known as the Bahia and Pernambuco refuge) remained, whereas, in southern Brazil, only small patches were predicted to occur (Carnaval et al., 2014; Costa et al., 2018). As temperature and humidity increased through time, rain and moist forests expanded to constitute the Atlantic Forest as we know it nowadays (Oliveira-filho & Ratter, 1995). Thus north–south floristic differentiation observed along the region is strongly determined by temperature and rainfall regimes.

To assess tree density per hectare for the different species along the climatic gradients within the Atlantic Forest domain, we used data from 623 tree phytosociological surveys, distributed from south to north of the Atlantic Forest biome plus forest intrusions into the neighboring Caatinga, Cerrado, and Pampa biomes (Oliveira-Filho et al., 2006). The surveys were chosen to embrace tree community data across considerable environmental gradients, both in terms of temperature and water deficit. The phytosociological surveys are part of the TreeCo database, version 4 (Lima et al., 2015). The surveys were used here to provide a sample of the communities distributed across the gradients of temperature (Figure 1a) and climatic water deficit (Figure 1b). In each phytosociological survey (hereafter, site), all trees and palms with stem diameter at breast height ≥ 4.8 cm were recorded. All sites had an area of at least 1 ha. Surveys from secondary and highly disturbed forests were not included based on information provided by the original authors of the studies.

2.2 | Climatic data

Each site was associated with a geographical coordinate, obtaining climatic information. To investigate the effects of temperature and water stress on tree species distribution, we used mean annual temperature (MAT) and maximum climatological water deficit (CWD) (Chave et al., 2014). The MAT (i.e., average monthly mean temperature over the 12 months of the year) was obtained during the period between 1950 and 1990, and MAT was extracted from layers with 100 m resolution provided by Alvares et al. (2015, 2013). For the three sites located in Paraguay and Argentina, MAT was extracted at 1000 m resolution from Fick and Hijmans (2017). CWD is calculated as the cumulative sum of the difference between monthly rainfall and monthly evapotranspiration over the months where evapotranspiration is greater than rainfall (Chave et al., 2014). The more negative the CWD values are, the greater the water stress in a given area is. CWD values were extracted at 2.5 arc-minute resolution layers generated from weather station data between 1960 and 1990 (Chave et al., 2014). MAT and CWD were weakly correlated ($r = 0.46$) (Figure S1).

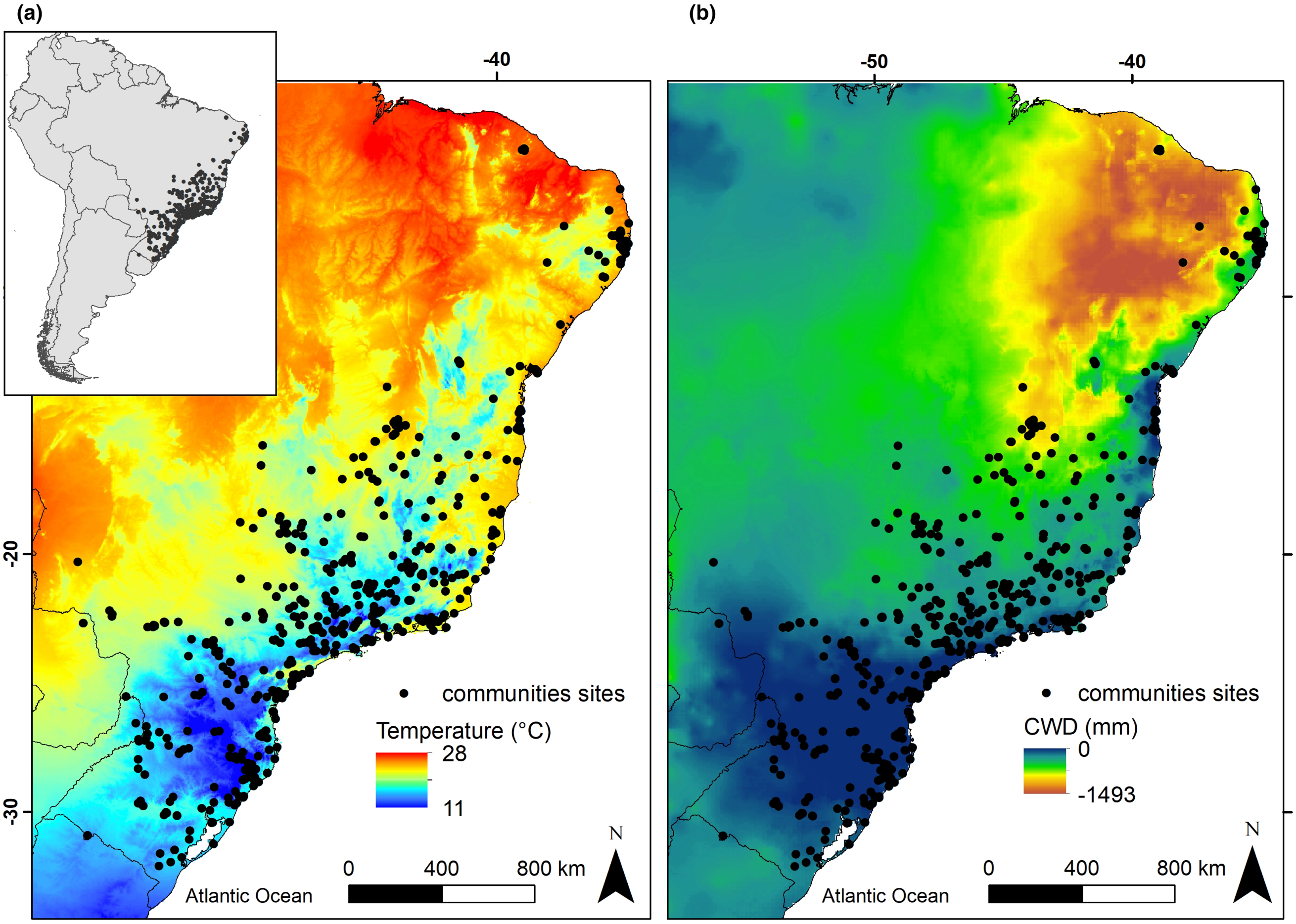

FIGURE 1 Location of the tree phytosociological surveys (623 sites) along the Atlantic Forest domain showing the distribution patterns of (a) mean annual temperature and (b) climatic water deficit in the background

2.3 | Niche optima and niche breadth

In this study, niche optima and niche breadth are based on the observed occurrence of species (i.e., realized niche) across both the climatic gradients of the studied region. Niche breadth is here indicated by climatic occurrence amplitude (either temperature or water deficit), that is, the range of maximum value minus minimum, whereas the niche optima consider the highest species abundance across the observed climatic occurrence, as explained in the sequence. We described the niche optima of each species to the temperature and water deficit by generating the "center of gravity" (CG) index (Chen et al., 2009). The CG value measures under which conditions the species achieves higher population density (niche optima) (Chen et al., 2009; Esquivel-Muelbert et al., 2016). The MAT center of gravity (TCG, Equation 1) and CWD center of gravity (CWD CG, Equation 2) are calculated as the mean of the climatic variable of locations where a given species occurs, weighted by the relative density of stems of that species in the corresponding site. To perform this analysis, we used only species with at least 10 occurrence records from the 623 surveys, which results in a total of 1138 tree species (Table S1).

$$TCG = \frac{\sum_1^n MAT * RD}{\sum_1^n AD} \tag{1}$$

$$CWD\,CG = \frac{\sum_1^n CWD * RD}{\sum_1^n AD} \tag{2}$$

where n = number of sites; MAT = annual mean temperature; CWD = climatic water deficit; RD = relative density per site (based on the number of trees of a given species per hectare). The resulting CG values are given on the same scale of the environmental variable assessed, that is, degrees Celsius for MAT and millimeters for CWD.

To quantify the niche breadth, we evaluated the species distribution range along the climatic gradients (occurrence amplitude) of MAT and CWD. To better capture the climatic range of species occurrence, we extended the information to all tree sites data available in the TreeCo database, including sites beyond the previous limits used to evaluate species abundance and forest surveys out from the previous inclusion criteria (i.e., 623 sites, see item 2.1). This resulted in 1853 sites. Then, each species had its niche breadth calculated considering the range between their upper and lower limits of occurrence within either the MAT or the CWD gradient.

2.4 | Data analyses

First, we run a non-metric multidimensional scaling (NMDS) ordination analysis using the whole matrix of sites by species density and depicted the species on the diagrams according to their CG values to explore general trends in species distribution, either for the temperature or the CWD variables. Before the analysis, data were submitted to the Hellinger transformation to minimize the effects of discrepant abundances. The NMDS ordination was performed using the function "metaMDS," package *vegan* (Oksanen et al., 2017). Then (aim i), the ranges of each species were plotted along the *y*-axis of MAT and CWD, considering the sequence order given by the range value for each variable (i.e., from the species with the larger niche breadth to the species with the smaller one). These graphs represent the range of the climatic condition in which each species occurs (e.g., from maximum to minimum MAT) and allow one to visually inspect the patterns of environmental ranges (niche breadth) among the studied species. Additionally, as we expect species that are more tolerant to drier conditions (distribution limit at more negative CWD) or to lower temperatures (distribution limit at lower MAT) to have wider climatic range size, we tested the relationships between species range and the climatic limit values (lower and upper limits) in which species occur using Kendall's τ coefficient of correlation (Hollander & Wolfe, 1973).

Second, we tested whether the species occurrence along the temperature and water deficit gradients in the 623 surveys follow a nested pattern (aim ii). The nestedness of species incidence across the studied environmental gradient was described by a statistic that varies from 0 (no nesting) to 100 (perfect nesting). The nestedness of the observed species occurrence data (not communities or the whole matrix) was compared against random distribution to assess whether the observed data had a higher degree of nesting than the one expected by chance. Simulation method "r1" was used with 1000 simulations to create a null model, which maintains the species richness of each site and thus assumes any significant nested pattern as a consequence of differences in species incidence, not richness (Almeida-Neto et al., 2008; Almeida-Neto & Ulrich, 2011). To perform this analysis, we used the functions "*nestednodf*" and "*oecosimu*" from "*vegan*" package (Almeida-Neto et al., 2008; Almeida-Neto & Ulrich, 2011).

Third, we investigated whether the species' measured CG matches with the expected niche optima if considering an even distribution of abundances across the climatic gradient, that is, the middle of the species' range occurrence (aim iii). Here, we used the range calculated earlier, extending the information to all site data in the TreeCo database (i.e., 1853 sites). We compared the expected CG value (i.e., the mean value within the interval between the upper and the lower climatic limit) with the observed CG, applying the Person's Chi-square test. Uneven distribution of the observed CG might be indicating greater vulnerability of species in the face of climatic changes.

Finally, we analyzed the affiliation of species to a particular environmental condition by testing the null hypothesis that the observed values CG for MAT and CWD differ from CG values calculated when the sites are placed randomly along with the temperature and the water deficit gradients (aim iv). We generated 999 null CG values for each species by shuffling the MAT and CWD values among the sites and calculated the probability of the observed CG being higher than the CG calculated using random values of MAT and CWD (Manly, 1997), using package *vegan* (Oksanen et al., 2017) in R (www.r-project.org). This process generated a distribution of two-tailed *p* values where a small value (<0.05) indicates that the taxon is significantly cold-affiliated or dry-affiliated, and a high value (>0.95) indicates warm-affiliated and wet-affiliated species. Then, we compared MAT and CWD ranges through t-tests between those species that were significantly affiliated to cold and warm temperatures and to dry and wet water conditions.

3 | RESULTS

The NMDS ordination of tree communities across the Atlantic Forest domain revealed the main variance in species composition associated with temperature and CWD. We combined the ordination result with the CG values of all species, and we saw that species with lower CG values for temperature are mostly associated with communities in the right upper portion of the diagram. In contrast, species with higher CG values for water deficit are in the left portion of the diagram (Figure 2). According to the distribution of these tree species, we have communities across a continuum gradient of temperature and water deficit, but the extreme conditions ("harsher") might be here characterized by cold-wet and warm-dry conditions.

The species distribution range along both gradients, MAT, and CWD (Figure 3), showed that most of the analyzed species occur in warmer and more humid places (right limits of both graphs). In contrast, a small subset of species tolerates colder and drier conditions (left limits of both graphs). Both subsets of species that tolerate colder and drier conditions have higher environmental ranges, that is, they are at the base of the graphs (Figure 3). These results are corroborated by range sizes showing stronger correlation with coldest (tau = −0.63, *p* <.01) and driest (tau = −0.89, *p* <.01) limit than with hottest (tau = 0.17, *p* <.01) and wettest (tau = 0.03, *p* <.01) limit (Figure 4). Moreover, we found weak evidence of a nested pattern in the species distribution across the climatic gradients (NODF (species) = 13.01, *p* <.01), with only a few species having a nested incidence pattern across the climatic gradients (Table S2).

The observed TCG did not differ from the expected CG (x^2 = 48.27; *p* = 1; Figure 5a), that is, the niche optima is almost at the center of the temperature range of each species. In contrast, the observed CWD CG differed significantly from the expected value given the occurrence range of the species (x^2 = 37,951; *p* <.01; Figure 5b); species show niche optima under wetter conditions than expected considering the center of their range.

Across all the 1138 species analyzed, 126 were significantly affiliated to temperature (Table S1), with 60 species being affiliated to lower temperatures (12–17 °C) and 66 affiliated to higher ones (24–26

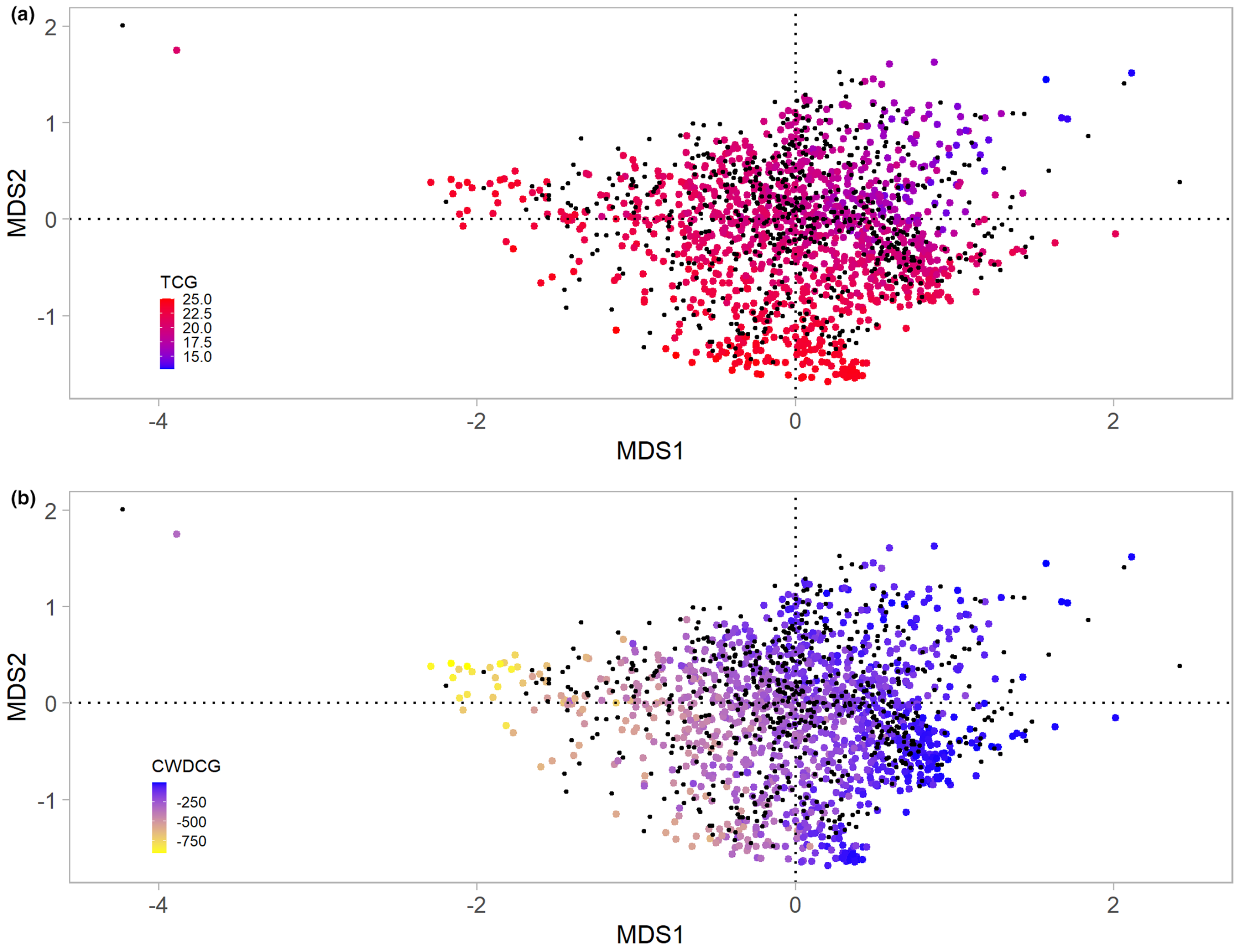

FIGURE 2 Ordination diagrams of the non-metric multidimensional scaling (NMDS) of 623 sites (black points) by 1138 species (color points) showing the general trends in species distribution across forest tree communities in the Atlantic Forest domain. Both figures represent the same ordination result, but the depicted colors of species represent the gradient of the center of gravity (CG) of each species to (a) temperature and (b) climatic water deficit (CWD)

°C) (Figure 6a). Cold-affiliated species showed larger niche breadth (*t* = 22.30, df = 65, *p* <.001) than warm-affiliated species (*t* = 55.35, df = 65, *p* <.001; Figure 6c). The CWD CG was significant for 126 species (Table S1), with 63 species being affiliated to dry conditions and 63 species affiliated to low/no water deficit regimes (Figure 6c). Significantly dry-affiliated species had larger niche breadth (*t* = 7.09, df = 62, *p* <.001) than wet-affiliated species (*t* = 9.28, df = 62, *p* <.001; Figure 6d).

4 | DISCUSSION

Our results demonstrated the influence of temperature and water deficit on the distribution and abundance of tree species in the Atlantic Forest domain. Across the broad environmental conditions of this mostly moist tropical forest region, we found sets of species having better performance (higher relative density) in communities under cold-wet and warm-dry conditions. The incidence and distribution patterns among these species that occur under harsher environments (in colder or drier conditions) were similar; they were widely distributed along the gradients, contrasting with those species restricted to warm or wet conditions with smaller ranges. These species that tolerate colder and drier conditions were small subsets of the analyzed pool rather than distinct sets of species with occurrence restricted to environmental challenging conditions because of their broader climatic range. However, the observed nested structure in species incidence had a relatively low value, evidencing that tree species associated with colder (e.g., in subtropical forests) and drier (e.g., in more seasonal forests) conditions are small subsets of the flora also present in warmer and moister tropical forests (Oliveira-Filho et al., 2013), which are richer in species and endemisms (Lima et al., 2020). Nested metacommunity structure was previously evidenced for trees either in a similar spatial scale (i.e., including distinct forest types across the Brazilian Atlantic Forest) or in smaller scales (within each forest type), but the nested structure was not perfect as clumped species

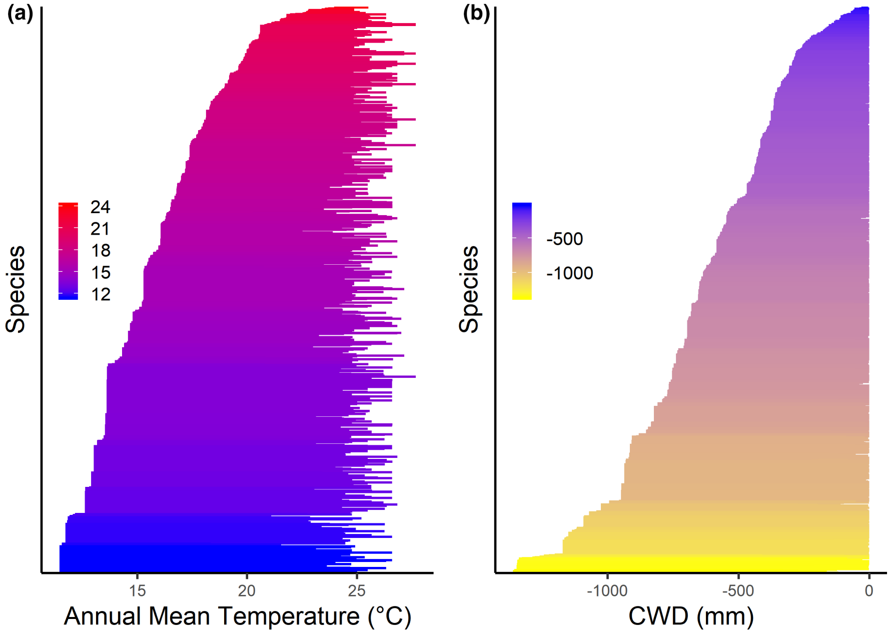

FIGURE 3 Niche breadth of 1138 species considering their occurrence range (lower and upper limits) across the studied environmental gradients: (a) annual mean temperature and (b) climatic water deficit. The *x*-axis represent the environmental gradients and the *y*-axis correspond to different species (lines), which are in a sequence order from the higher range value to the smaller one. The colors represent gradients from harsher to milder conditions based on one of the limits of occurrence: colder for (a) temperature and drier for (b) climatic water deficit (CWD)

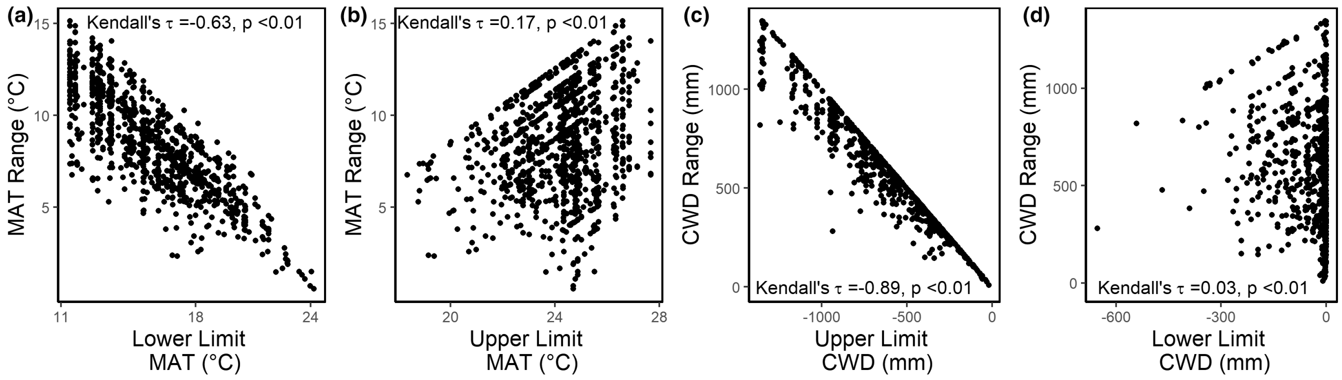

FIGURE 4 Niche breadth (climatic range) and the occurrence limits of all 1138 tree species along the climatic gradients. Scatterplots and correlations show the relationships from temperature range (MAT Range) (a, b) and from maximum CWD range (c, d) against the lower and upper climatic limits that each species occur

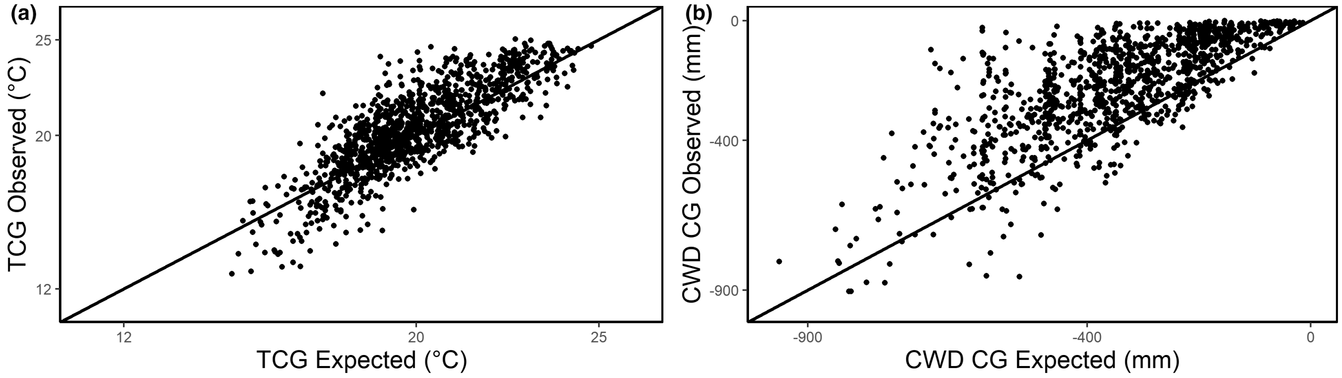

FIGURE 5 The relationship between niche optima (CG values) and the mean value of species' range occurrence. Deviation from 1:1 line plots from temperature center of gravity observed (TCG) (a) and maximum CWD center of gravity observed (CWD CG) (b) against the center of gravity expected. TCG observed was not significantly different from the TCG expected. In contrast, CWD CG observed differed significantly from the CWD CG expected ($p < .01$), indicating that the species have an optimal climate in less water deficit conditions than expected

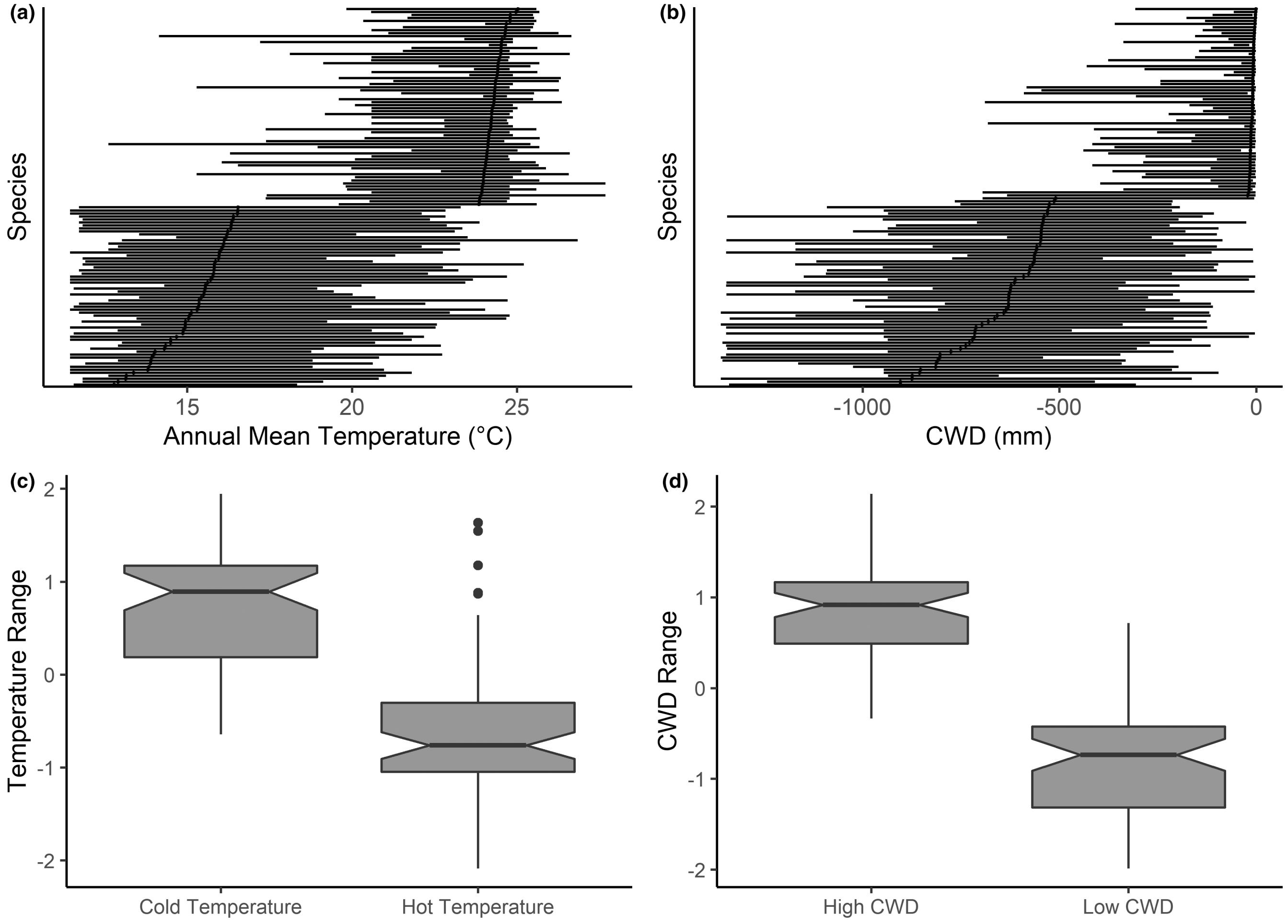

FIGURE 6 Distribution ranges (niche breadth; lines) and optimal niches (points) of species significantly affiliated to temperature and CWD gradients. Annual mean temperature (a) and climatic water deficit (b). Graph (c) represents temperature range contrasts between species significantly affiliated to cold and hot conditions; whereas in (d) the contrasts are between species significantly affiliated to wetter (low CWD) and to drier (high CWD) conditions. Values of temperature and CWD were standardized to zero mean and unit variance to allow a better comparison; both *t*-tests showed significant differences ($p < .001$) between species groups

loss occurs toward regions of more limited environmental requirements (Marcilio-Silva et al., 2017).

Temperature is a relevant driver of forest tree species distribution. Out of the many species that are widely distributed in tropical regions, only a few have successfully radiated to colder areas (e.g., Giehl & Jarenkow, 2012; Oliveira-Filho & Fontes, 2000), potentially due to their lack of tolerance to frost (Araújo et al., 2013; Donoghue, 2008). In this context, we showed that most Atlantic Forest tree species occur in warmer places with a restricted tolerance to temperature conditions. We also observed that temperature CG did not differ from the expected value, overall indicating the higher performance of species (i.e., abundance) in forest sites which MAT is close to the center of species temperature breadth. However, we clearly observed some species presenting higher tolerance to different temperatures, from cold to warm temperatures (large niche breadth), and these are especially cold-affiliated species. These results reinforce the suggestion that some tropical lineages that originated in the tropical regions expanded their occurrence toward colder areas (Pennington & Dick, 2004), as cold tolerance is thought to have evolved only in a few clades (Wiens & Donoghue, 2004). And this is corroborated by the analysis of species composition patterns of forests in the southern limit of the Atlantic Forest, under a subtropical climate (Neves et al., 2017; Oliveira-Filho et al., 2013). Therefore, even with larger occurrence breadth, cold-tolerant species have higher abundance under lower temperatures, probably because of their adaptive traits and consequent benefits to coexistence in local biotic interactions (Abeli et al., 2014; Dallas et al., 2017; Sporbert et al., 2020).

As expected for the Atlantic Forest region, almost all tree species occur in sites without climatic water deficit and under warm temperatures. Most tropical tree species might coexist under such favorable conditions, where a wider range of functional strategies is expected (Spasojevic et al., 2014). But we further found a smaller proportion of species occurring with higher densities under drier conditions. Tree species that manage withstanding long dry seasons might be associated with seasonal forests (Scarano, 2009), having ecological strategies, such as deciduousness (Eamus, 1999) or maintenance of living tissues under more negative water potentials (Baltzer et al., 2008), which in turn can lead to local high densities (Eisenlohr & de Oliveira-Filho, 2015). On the other hand, we observed that niche optima (represented here by CG) of species is under wetter conditions than expected by the center of the water-deficit range, showing that water deficit is a strong stress condition for the abundance distribution of Atlantic Forest tree species. Thus, expected changes in precipitation regimes toward droughts over this broad tropical region might profoundly affect forest functioning due to shifts in traits and species abundance distribution, which in turn influence the mechanisms of coexistence in ecological communities.

Our study results also highlight that species affiliated with high temperature or those with low water deficits have their niches optima near to their limits of MAT and CWD gradients and not in the middle of species climatic ranges. In addition, they also have small niche breadths, which make these species more susceptible in the face of future global warming changes. Recent increases in the frequency of extreme temperatures have been especially pronounced in the tropics (Buckley & Huey, 2016), and what is currently considered extreme for the tropics is projected to become normal by the end of the century (Battisti & Naylor, Battisti & Naylor, 2009). Then, rising mean temperatures and droughts can reduce species' abundance in the hotter and drier limits of their ranges and increase in their currently colder and wetter limits. Additionally, some studies show a decrease in the relative abundance of wet-affiliated species in regions where the climate has become drier, leading to a shift in species composition toward a more dry-affiliated community (Esquivel-Muelbert et al., 2018; Feeley et al., 2020). This highlights that we need to refine our predictions of climate change impacts since the demographic response may not be the same on both sides of the tolerance limits and because these limits vary among species and forest types.

It is not new that climate change is shifting biodiversity by causing shifts in species distributions, community composition, and ecosystem function (Bertrand et al., 2016; Peterson et al., 2019; Zimmermann et al., 2009). The persistence of species under future climate depends on their tolerance to climatic stresses, on the capacity to shift their climatic niche (Bertrand, 2018), and on the ability to migrate fast enough to keep pace with the rapidly changing climate (Alexander et al., 2018; Renwick & Rocca, 2015). Climate change scenarios project an increase in rainfall irregularities (i.e., longer drought periods) over the next decades (IPCC, 2021). Also, an increase in mean temperature is expected for Neotropics and a reduction in frost frequency toward subtropical areas (Marengo, 2014). Therefore, species composition and diversity of tree communities, especially due to changes in incidence and density, may substantially change in the long term (Raymundo et al., 2019) with a steady decrease in the density of cold-affiliated species in the subtropical region and wet-affiliated species in the tropical region. However, predicting future distributions and abundances of tropical and subtropical species remains uncertain (Bertrand, 2018), especially because evolution could alter species responses to climate change at the edge of the range and since these regions are often the first to experience novel selection (Nadeau & Urban, 2019; Rehm et al., 2015). Furthermore, an increase in the density of generalist species is expected, potentially leading to biotic homogenization of biodiversity along with the remnants of forests (Zwiener, 2017).

Our study contributes to the understanding of species distribution across climatic gradients, which can help us understand species tolerances and predict the effects of droughts and temperature rise on species composition of forests. Although we considered that species had only one optimal climatic condition (i.e., the unimodal response of niche), our results are relevant to understanding how temperature and water deficit increases might affect tree species composition in the Atlantic Forest. We clearly showed that tree species tolerating harsher conditions in the studied region (colder or drier sites) have a large distribution range along the gradients. However, most of the studied tree species have narrow climatic niches being limited within warm and wet conditions, and these might be particularly vulnerable in the context of global changes. If their niche breadth represents their tolerance, their existence within this biome may be at risk even by small climatic shifts. On the other hand, cold-affiliated species with wide niche breadths may lose their competitive advantage as the temperature rises to release the limitation imposed on other more warm-affiliated species. Maintaining remnants and increasing forest corridors are essential measures to allow tree species to acclimatize and/or potentially migrate to more favorable conditions in the face of climate change.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data underlying CG values and climatic ranges presented in the figures are available in the supplementary information accompanying this paper. Raw data on species abundance used in this study are stored in Neotropical Tree Communities (TreeCo) database and are available upon request from the corresponding author or directly on the site (http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start).

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