Climate change might lead to substantial niche displacement in one of the most biodiverse regions in the world

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Abstract

Climatic niches are key factors driving global and regional species distributions. The Atlantic Forest domain is considered one of the most threatened biomes in the world, and one of the main centres of plant diversity and endemism in the Neotropics. Of the over 13,000 species of vascular plants, nearly 15% are vascular epiphytes. Here we analysed for the first time how current epiphyte niches will be affected under future climate projections (SSP126 and SSP585) within 1.5 million km^2 of Atlantic Forest in South America. Using the largest database of vascular epiphytes to date (n = 1521 species; n = 75,599 occurrence records) and ordination models, we found that the Atlantic Forest is expected to become warmer and drier and that up to 304 epiphyte species (20%) will have their average niche positions displaced outside the available climate space by the years 2040–2100. The findings from this study can help to inform ongoing legislative conservation efforts in one of the world's most biodiverse regions.

Keywords Epiphyte · Orchids · Bromeliads · Ferns · Climate Change · Atlantic Forest

Introduction

Climate change is already causing species range shifts, local species loss and mass extinction events globally (IPCC 2022). Changes in temperature and precipitation has caused species to shift to areas of more suitable conditions, consequently altering their distributions, both locally and across continental scales (Bellard 2012; Pecl et al. 2017). However, species that have restricted distributions and/or greater sensitivity to environmental disturbances may not find new habitats that are suitable for them in the future, thus becoming more vulnerable and are at greater risk of extinction (Ruegg et al. 2021). In particular, stochastic and local disturbance events, such as droughts, disease outbreaks, and land use changes, may accelerate the extinction of species with smaller distribution ranges (Thuiller et al. 2005; Lawton 1995). In both cases – range shift and extinction – can

lead to changes in the composition of local and regional communities, and might result in generalists and more tolerant species numbers to increase compared to more sensitive species (Baselga 2010; Spaak et al. 2017; Hidasi-neto et al. 2019; Mota et al. 2022). Climate change may thus impact not only individual species or groups of organisms, but also alter ecological functions with ecosystems (Galetti et al. 2013). Understanding species responses to changes in climate is thus crucial for building effective preventive measures and support conservation efforts (Stanton et al. 2014).

The use of climatic niche-based approaches has been shown to be a suitable strategy to assess species' response to climate change (Pie et al. 2022). Climatic niches are the set of climatic conditions linked to the occurrence of a species. The focus on a subgroup of climatic variables, instead of assessing all biotic and abiotic dimensions, in an n-dimensional hypervolume of Hutchinson's ecological space (Hutchinson 1957), makes it both a practical and heuristic approach (Pie et al. 2022). Climatic niche studies also provides an intersection of many diverse fields, including ecophysiology, invasion biology, biogeography, and macroecology (Petitpierre et al. 2012; Khaliq et al. 2015; Wasof et al. 2015; Atwater et al. 2018). Moreover, it is a key component of phylogenetic niche conservatism (Wiens and Donoghue 2004), which has been pivotal to understand the

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biogeographical distributions of many species, as well as the origin of latitudinal gradients of species diversity (e.g., Buckley et al. 2010; Kerkhoff et al. 2014).

The South American Atlantic Forest (AF) is considered one of the most endangered ecosystems in the world (Myers et al. 2000; Mittermeier et al. 2004); with nearly 95% of forest occurring in eastern Brazil and the remaining 5% occurring in Argentina and Paraguay (Marques et al. 2021). The AF covers an area of 1.5 million km^2. However, only 12% of the original cover remains intact, with the remaining forest being fragmented (Ribeiro et al. 2009). Nevertheless, the mosaic of remaining native forest (incl. non-forest ecosystems) harbours over 16,000 species of land plants (Forzza et al. 2012). The biological diversity of this domain is believed to be driven by the regions geographic, geologic, and climatic heterogeneity; where it presents great latitudinal (3°S–30°S), altitudinal (0–2,800 m a.s.l.), and rainfall gradients. The latter is characterized by distinct seasonality in continental interior formations (~ 1,000 mm/year during the wet season), and higher precipitation in coastal forests (4,000 mm/year) (Câmara 2003). This heterogeneity has resulted in the establishment of both forests and open vegetation within the AF (Stehmann et al. 2009). In addition, approximately 47% of the plant species found in the AF are endemic to the domain (Forzza et al. 2012). The high level of endemism is associated with the isolation of wetter vegetations by dry open formations (e.g. Caatinga, Cerrado, and Chaco) from the Amazon, the Easter Andean forests and the Choco region in Colombia's Pacific Coast (Zanella 2011), to the major humid forest formations in South America.

Vascular epiphytes, which are mechanically dependent plants that lack connection to the ground (Zotz 2016), and in some cases obtain their nutrients from atmospheric sources (Benzing 1990), are a conspicuous group of plants in the AF. Within the AF, vascular epiphytes account for over 2,000 species (Ramos et al. 2019), of which 78% are endemic to the domain (Freitas et al. 2016). Families such as Orchidaceae (79%), Gesneriaceae (89%), and Bromeliaceae (91%) show a particular high degree of endemism (Ramos et al. 2021). Because of their tight coupling to atmospheric conditions, epiphytes are believed to be particularly vulnerable to climate change (Zotz and Bader 2008). For example, it has been shown that sensitive epiphytes species in other parts of the world are more geographically restricted and their distribution is believed to be stronger related to changes in temperature (Hsu et al. 2012). It has also been suggested that epiphytes are more vulnerable than terrestrial species in the future (Reyes et al. 2021). Despite that, little is known about the effect of climate change on vascular epiphytes in the AF and across large geographical scales.

Therefore, this study aims a) to use high spatial resolution data of temperature and precipitation to describe the structure of the available climatic conditions across the AF; b) to

determine the extent to which the available climatic space is occupied by different vascular epiphytes; c) to assess which regions of the climatic space will be most/least affected under different climate change scenarios; and d) to quantify which group of vascular epiphytes are under greater risk of niche displacement in the future. The findings of this work will support current legally binding conservation efforts (incl. the Brazilian National Atlantic Forest Law), to better understand current and future species distributions of one of the most diverse plant groups in the AF.

Materials and methods

Occurrence data

Vascular epiphyte occurrence data were extracted from Ramos et al. (2019) and de Araujo and Ramos (2021). These datasets comprised 2,095 species of structural dependent plants from 79,464 individual records (Fig. 1). The original data was compiled from published sources (comprising peer-reviewed articles, books, and theses), unpublished data, and herbarium records, spanning from 1815 to 2018. The geographical extent of the original data included countries such as the AF of Brazil, Argentina, and Paraguay. All non-vascular species were excluded. We used Flora do Brasil (Flora do Brasil 2020) and Zotz et al. (2021) to cross-reference epiphytic life-forms against our database. We retained any species classified as epiphyte in at least one of the reference databases.

Since many vascular epiphyte species are naturally rare, we also wanted to test if the displacement of a species was related to its number of records in the dataset, thus we generated three different datasets (e.g. C10, C5, and C3) in accordance to the minimum number of records per species (C10 = ten or more records; C5 five or more records; C3 three or more records). Following the removal of any species that did not match the occurrence criteria in each database, we retained 72,798 records from 1000 species for database C10, 74,882 records from 1312 species for database C5, and 75,599 records from 1,521 species for database C3.

Climatic variables

In order to build the environmental matrix, climate data was extracted from the 19 standard bioclimatic variables from WorldClim 2.1 database (Fick and Hijmans 2017) for the period between 1970 and 2000 at a spatial resolution of 30 s. Following Pie et al. (2022), a Principal Component Analysis was used, based on a covariance matrix of the 19 bioclimatic variables, which were scaled and centred prior to the analysis and retained for the first two axes. Our next step was to extract bioclimatic data from vascular epiphyte occurrence

Fig. 1 The records of vascular epiphytes according to Ramos et al. (2019) and de Araujo and Ramos (2021) within the Atlantic Forest domain

records using 'raster' 3.4–13 package (Hijmans 2021) and project them onto the first two axes of the principal components retained for the analysis. To investigate the extent of the occupancy of different species across the climate space, we compared the variance across ordination quadrants using Levene's test, incorporated into 'car' 3.0–11 (Fox and Weisberg 2019). By using the predictions in the Met Office Hadley Centre (UK) model–ukesm1-0-ll (2020), we explored how expected shifts due to climate change might affect the structure of the available climatic space. We used two SSP (e.g., Shared Socioeconomic Pathway) from the IPCC AR6 (e.g., 6th Intergovernmental Panel on Climate Change Assessment Report) climate change projections.

SSP126, hereafter the optimistic scenario, forecasts global temperatures assuming atmospheric CO_2 emissions will be cut to net zero in the year 2075, keeping global warming below 2 °C by 2100. SSP585, hereafter the pessimistic scenario, assumes that CO_2 emissions will triple by 2075 and the increase in global temperature will be between 3.3 and 5.7 °C by 2100. We extracted the values of the above climate variables for each grid cell and designed them based on the PCA constructed with the current climate data. By estimating concave hulls, as implemented in 'concaveman' 1.1.0 (Gombin et al. 2020), we compared the extent of the corresponding climatic space. This approach allowed us to assess which regions of the climatic space harbour more species

that are likely to have their climatic niche displaced in the future. All analyses were carried out in RStudio 2022.07.1 (R Core Team 2022) and maps were plotted in QGIS 3.16.14 (QGIS Development Team 2022).

To test whether the niche displacement of a species would be related to the number of records of that species in each dataset, we performed a logistic regression between the number of displaced species and its number of occurrences in the datasets using the glm function in R (R Core Team 2022; version 4.2.1). This was done separately for the C3, C5, and C10 datasets. The logistic regression analysis did not have its assumptions met by the data for the SSP126 scenario, probably due to the imbalance between the categories of the response variable (e.g. few entries of displaced species versus many entries of non-displaced species in this scenario). However, for SSP585 the logistic regression showed that there was no significant effect of the abundance of records of a species and the number of displaced species (Std. Error = 0.0008672; z value = -1.13; Pr(>|z|) = 0.26). This suggests that the lower number of records of some species did not necessarily imply that these species will be more likely among the species with their climatic niche displaced. Thus, any further analysis was performed on the C3 dataset only.

Finally, to test whether there was a difference between climate changes scenarios (SSP126 and SSP585) and the number of species found in different climate space regions as identified by the ordination analysis (e.g. warmer regions vs. cooler regions), a chi-square test was carried out using the chisq.test function in R (R Core Team 2022).

Results

The first two axes of the PCA explained 69% of the variance in climatic conditions across the AF. The first axis, which explains 49% of the data variance, was mainly related to mean air temperature, especially during colder months (e.g. June to August). The second axis, which accounted for 20% of the total variance, was mainly related to the precipitation, especially during the wet and warmer months (Table 1).

The broad distribution of species across most of the available climatic space indicates that vascular epiphytes tend to thrive in climatic conditions currently found throughout the AF (Fig. 2). The ordination climate space analysis suggests two distinct climate area across the AF; one with higher temperatures and lower precipitation (PC1-; PC2+), hereafter referred to as the harsher zone, where the occurrence of epiphytes appears to be more restricted to species within Bromeliaceae, and a region of relatively lower temperature and higher precipitation (PC1+, PC2-), here referred to as the milder zone, more occupied by other epiphyte families (Fig. 2). Among the 1,521 analysed species, 324 (21.3%) had their mean climatic occurrence within the harsher zone,

Table 1 Principal Component Analysis of bioclimatic variables found in the AF

Variable	PC1	PC2
Mean annual air temp	**− 0.30**	0.13
Mean diurnal air temp range	− 0.02	− 0.23
Isothermality	− 0.27	− 0.13
Temperature seasonality	**0.28**	0.09
Mean daily maximum air temperature of the warmest month	− 0.22	0.17
Mean daily minimum temperature of the coldest month	**− 0.28**	0.20
Annual range of air temperature	0.17	− 0.11
Mean daily mean air temperatures of the wettest quarter	− 0.24	0.01
Mean daily mean air temperatures of the driest quarter	− 0.26	0.20
Mean daily mean air temperatures of the warmest quarter	− 0.23	0.22
Mean daily mean air temperatures of the coldest quarter	**− 0.32**	0.09
Annual precipitation amount	0.24	− 0.05
Precipitation amount of the wettest month	− 0.02	− 0.40
Precipitation amount of the driest month	0.27	0.24
Precipitation seasonality	− 0.25	**-0.31**
Mean monthly precipitation amount of the wettest quarter	− 0.02	− 0.40
Mean monthly precipitation amount of the driest quarter	0.27	0.24
Mean monthly precipitation amount of the warmest quarter	0.14	**− 0.35**
Mean monthly precipitation amount of the coldest quarter	0.19	**0.28**
Proportion of variance	**0.49**	**0.20**
Cumulative proportion	**0.49**	**0.69**

Bold numbers indicate the variables that contributed most to axis 1 and 2 respectively
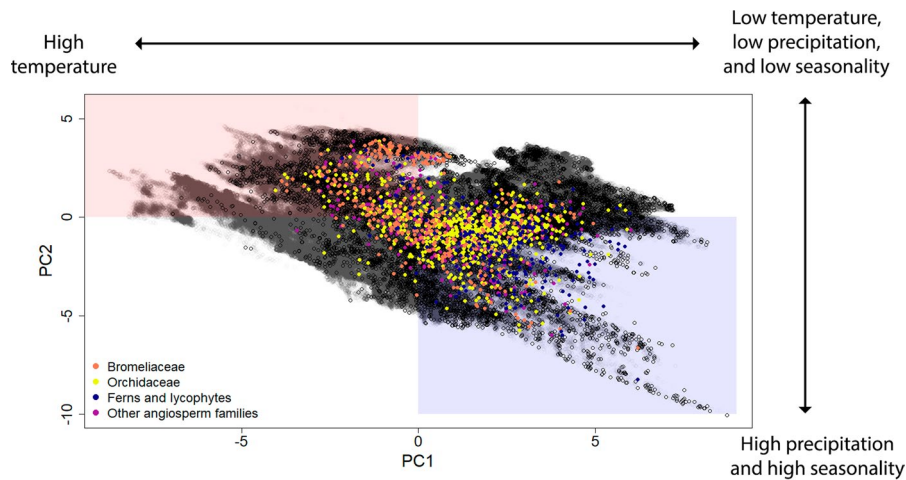
Fig. 2 Principal component analysis of climatic conditions found in the AF. Gray circles show the climatic conditions. Occurrence of the different epiphyte species across the available climate space for the main epiphytic groups (e.g. Bromeliaceae, Orchidaceae, ferns and lycophytes and other angiosperm families) are shown in different col- ours. Closed circles represent species means and black open circles indicate individual records. The arrows describe the general climate space (see text for details). Red and blue rectangles show the harsher and the milder zone respectively. (Color figure online)

831 (54.6%) had their mean climatic occurrence within the milder zone, and 366 species (24.1%) had their mean climatic occurrence outside the harsher and milder zone (Fig. 2).

When projecting the PCA scores back cartographically (Fig. 3A, B), the lowest temperatures (Fig. 3A) were found in the southern part of the AF, especially in Argentina and Paraguay, as well as in the Brazilian southern states of Paraná, Santa Catarina, and Rio Grande do Sul. On the other hand, the central AF had warmer average temperatures. Lower temperatures were found in the higher regions of the Serra do Mar mountains, across the Brazilian states of Minas Gerais, São Paulo, Rio de Janeiro, and Espírito Santo. The purple band that extends across the interior of the Brazilian states of Minas Gerais, Bahia, and Piauí reflects the greater seasonality of temperature in the interior area of the Atlantic Forest, despite its relatively lower mean annual temperatures. Precipitation and seasonality patterns are notable from the purple regions across southern Brazilian states and on the south-eastern Brazil highland areas (Fig. 3B), indicating higher levels of precipitation. The purple hue that extends from southern Brazil to Minas Gerais state reflects local seasonality in precipitation (Fig. 3B).

In quadrants with negative PC1 scores, species were less frequent and lied further to the boundaries of the available niche space. Variance was higher across the available niche space in cooler conditions (i.e., positive PC1 scores) than in warmer conditions (i.e., negative PC1 scores) ($F = 6.28$, $p = 0.01229$). It is important to note that this difference was not a by-product of the variances of the available climatic space when they compared in a similar manner (4.1 vs. 3.6, respectively). We found higher variance values when comparing regions with low annual precipitation (i.e., positive PC2 scores), with areas of high annual precipitation (i.e., negative PC2 scores) ($F = 44.73$, $p = 3.168\text{e-}11$). However, in this case, the difference could not simply be explained by differences in the available climatic niche space (11.3 vs. 6.8, respectively).

When comparing the entire available climatic space, there were significant differences among the studied groups (i.e., Bromeliaceae, Orchidaceae, ferns and lycophytes, and other angiosperm families) in their pattern of occupation (Table 2; Fig. 2), with ferns and lycophytes and orchids showing smaller variance in their climatic niches and Bromeliaceae presenting the larger variance in its occupation pattern (Table 2). Bromeliaceae largely occupies most of the available climatic space, but it is mostly associated with warmer regions (negative PC1). On the other hand, Orchidaceae, despite occupying most of the climatic space, have a higher number of occurrences in areas that represent positive PC1 and negative PC2 scores (i.e. milder temperatures + higher precipitation). Ferns and lycophytes were the groups with the most restricted occurrence across the climate space. Species of these groups are mostly related to milder temperature and humid areas (i.e. positive PC1 + negative PC2), many of which are close to the edge of the available climatic space.

Climate projections for the years 2040 to 2100 for the optimistic (SSP126) and the pessimistic scenarios (SSP585), showed large climate niche shifts in the AF (Fig. 4). In general, the climate space will shift to hotter and drier conditions, with SSP585 projections showing the strongest shift (Fig. 5 and Fig. 6). Up to 20% of the analysed species will have their current average climatic niche outside future climatic spaces by 2100 (Table 3). This result is not due to a reduction in available
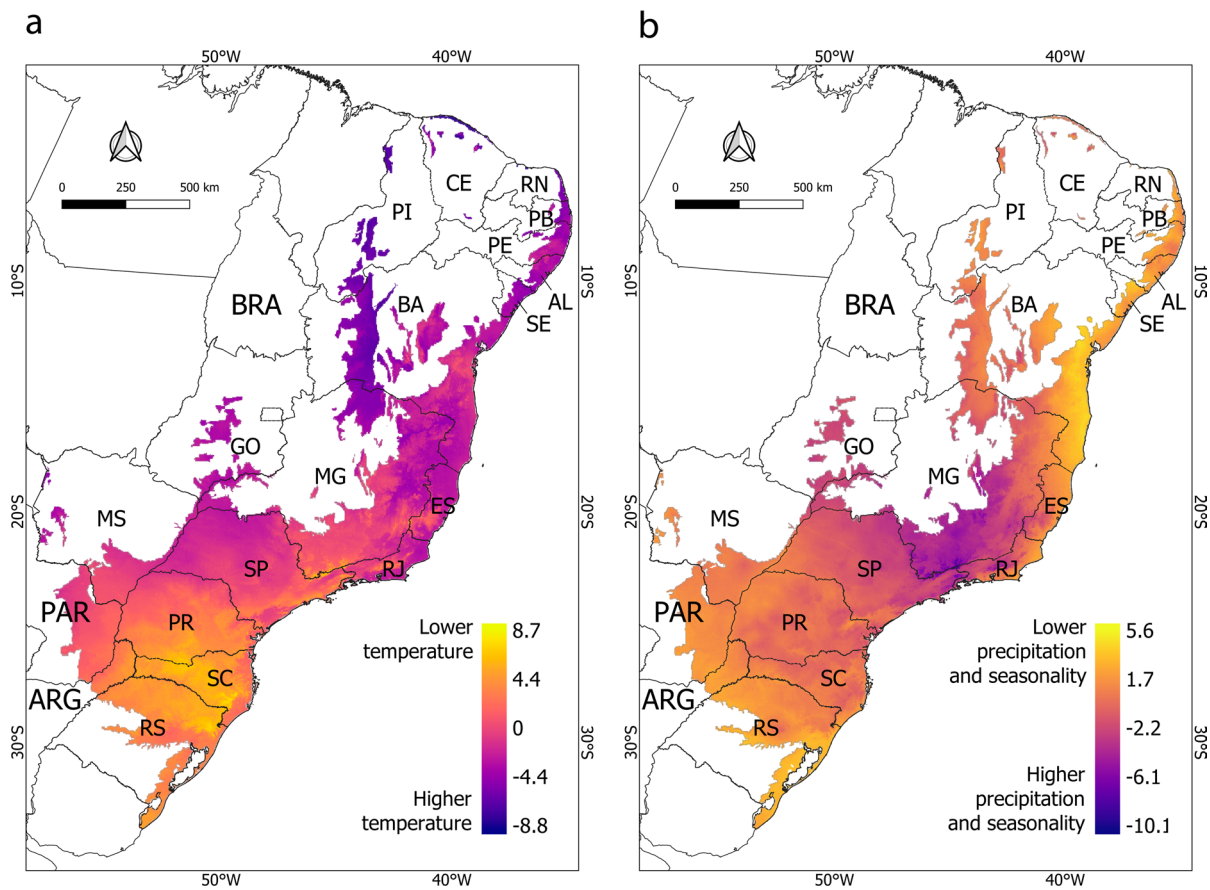
Fig. 3 Spatial distribution of component scores of the climatic conditions across the AF. To visualize the climate conditions associated with each grid cell, a principal component analysis was performed, and the results were mapped back to the corresponding cells. PC1 loadings mostly reflected variation in temperature (**a**), while PC2 described mostly precipitation (**b**). *ARG* Argentina, *BRA* Brazil, *PAR* Paraguay; Brazilian states: *AL* Alagoas, *BA* Bahia, *CE*=Ceará, *ES* Espírito Santo, *GO* Goiás, *MG* Minas Gerais, *MS* Mato Grosso do Sul, *PB* Paraíba, *PE* Pernambuco, *PI* Piauí, *PR* Paraná, *RJ* Rio de Janeiro, *RN* Rio Grande do Norte, *RS* Rio Grande do Sul, *SC* Santa Catarina, *SE* Sergipe, *SP* São Paulo

Table 2 Variance in the scores along different ordination axes of occupied climatic niche space of different epiphyte groups

Variable	Bromeliaceae	Ferns	Other Angiosperm families	Orchidaceae	F	P
PC1	3.05	2.9	3.02	3.33	1.82	0.14
PC1 (PC2+)	2.93	4.35	3.83	3.39	5.24	0.00
PC1 (PC2-)	1.97	1.72	1.88	2.29	2.38	0.07
PC2	4.56	2.15	3.65	3.12	26.05	0.00
PC2 (PC1+)	4.29	1.61	2.76	2.29	21.72	0.00
PC2 (PC1-)	2.78	2.2	2.18	2.13	2.53	0.06

"PC1 (PC2+)" and "PC1 (PC2−)" correspond to variance between different epiphyte groups on PC1 separately for higher precipitation seasonality (positive PC2 scores) and lower precipitation seasonality (negative PC2 scores), respectively. "PC2 (PC1+)" and "PC2 (PC−)" correspond to variance between epiphyte groups on PC2 separately for colder (positive PC1 scores) and warmer (negative PC1 scores), respectively

climatic space, but due to a mismatch between present and future climatic spaces (Table 3 and Fig. 5). In general, the proportion of impacted species is larger for Orchidaceae, ferns and lycophytes compared to Bromeliaceae (Table 3). Under projections for the optimistic scenario, however, Bromeliaceae was the group with higher percentage of displaced species, while the pessimistic projections seem to affect ferns and lycophytes more. It is important to note that there were two

Fig. 4 Principal component analysis of climatic conditions found in the AF, including climate space projections under SSP126 and SSP585 for the years 2040–2100. The different coloured lines represent different climate scenarios and years, whereas the different coloured open circles represent different epiphyte groups
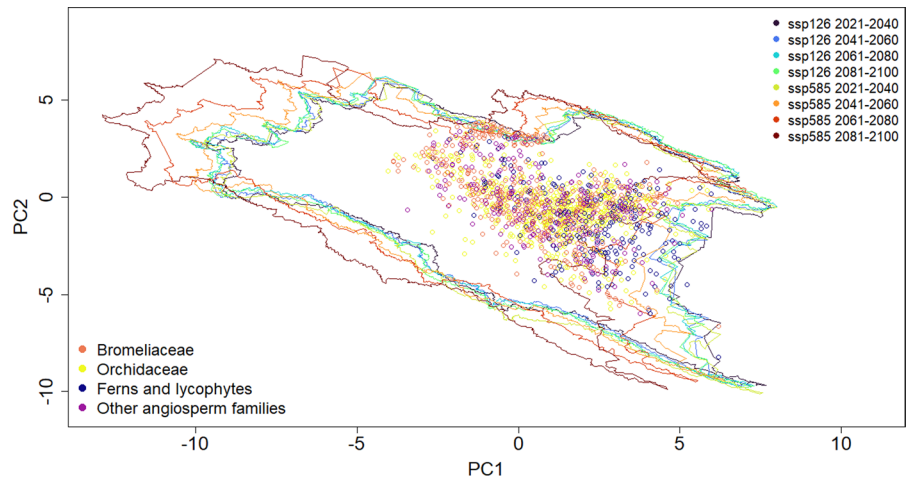
species (i.e. *Hymenophyllum crispum* Kunth and *H. magellanicum* Willd.) that were indicated as outside the present climatic space. As suggested by Pie et al (2022), those were species living near the boundaries of the present climatic space but were categorized to be outside because of the way that concave hull was computed. They were left to ensure that all comparisons were carried out using the same context.

Despite the harsher zone's geographical location in the lowlands, which extend from Paraguay to Brazilian Northeast (Fig. 5) (307 m ± 141 m asl.; 22.46 °C ± 1.02 °C), all the potentially displaced species (234 m ± 108 m; 23.14 °C ± 0.69 °C) are found in the north-eastern coast, with most of them being found in Bahia state (Fig. 5). In the milder zone, which geographically corresponds to mid-elevation areas (694 m ± 227 m asl.; 18.5 °C ± 1.15 °C), most displaced species are found in higher altitudes (969 m ± 218 m asl.; 17.06 °C ± 0.95 °C).

The χ-square test ($\chi^2 = 48.46$; p-value $= 3.372e-12$) revealed that species whose climatic mean is located in the harsher-zone are more sensitive to smaller shifts in their available climatic space compared to species on other zones (e.g. changes predicted for the optimistic scenario).

Discussion

Our analysis suggests that the climate space of the AF will get hotter and drier in the next 20–80 years. In addition, 10–35% of the currently climatic space will shift. These findings are in line with the latest IPCC assessment report for South America (IPCC 2022), which suggested that temperature in all South America subregions will most likely increase at rates greater than the global average. Precipitation, however, has been predicted to be more variable and regionally specific. While there is an expected decrease in precipitation in the harsher zone (i.e. the northern part of the AF), the milder zone (i.e. the southern part of the AF) will most likely experience an increase in precipitation according

to IPCC predictions (IPCC 2022). In addition, the intensity and frequency of extreme precipitation and floods are projected to increase in the southern parts of the AF, whilst the northern parts will likely experience an increase in intensity of droughts (IPCC 2022).

We identified two prevalent climate spaces; a harsher (hot and dry) and milder (cold and humid) zone, which corresponds mostly to the northern and southern parts respectively of the AF. This north/south climate division has previously been reported in terms of differences in species diversity and composition for many organisms (Amorim and Pires 1996; Oliveira Filho and Fontes 2000; Pellegrino et al. 2005; Cabanne et al. 2007; Ledru et al. 2007; Thomé et al. 2010; DaSilva and Pinto-da-Rocha 2011; Dasilva et al. 2015), including epiphytes (Menini Neto et al. 2016). It has been suggested that the Doce River valley in northern Espírito Santo represents a dispersal barrier for many species between the south and the north of the AF.

We found that almost 300 (20%) epiphyte species may have their mean climatic niche displaced under future climate change projections, many of which seem to be more climate sensitive species or species that are already at their climate limit. For example, groups with the highest numbers of displaced species were bromeliads, ferns, and lycophytes. Interestingly, the lowland forests of the northern region of the AF, which is hot and dry, appeared to harbour a subset of species which are less tolerant to climate change; as it presents similar number of displaced species, both for the optimistic (n = 36; 11% of the species within the harsher zone) and the pessimistic scenario (n = 39; 12%). Concerning the southern region of the AF, which is cold and humid, our results suggests that it will be less affected under optimistic (SSP126) climate change predictions (n = 27; 3% of the species within the milder zone) compared to the harsher zone. However, under pessimistic predictions (SSP585), the shift in climate niche space within the milder zone leads to an increase of displaced species nearly eight times to that
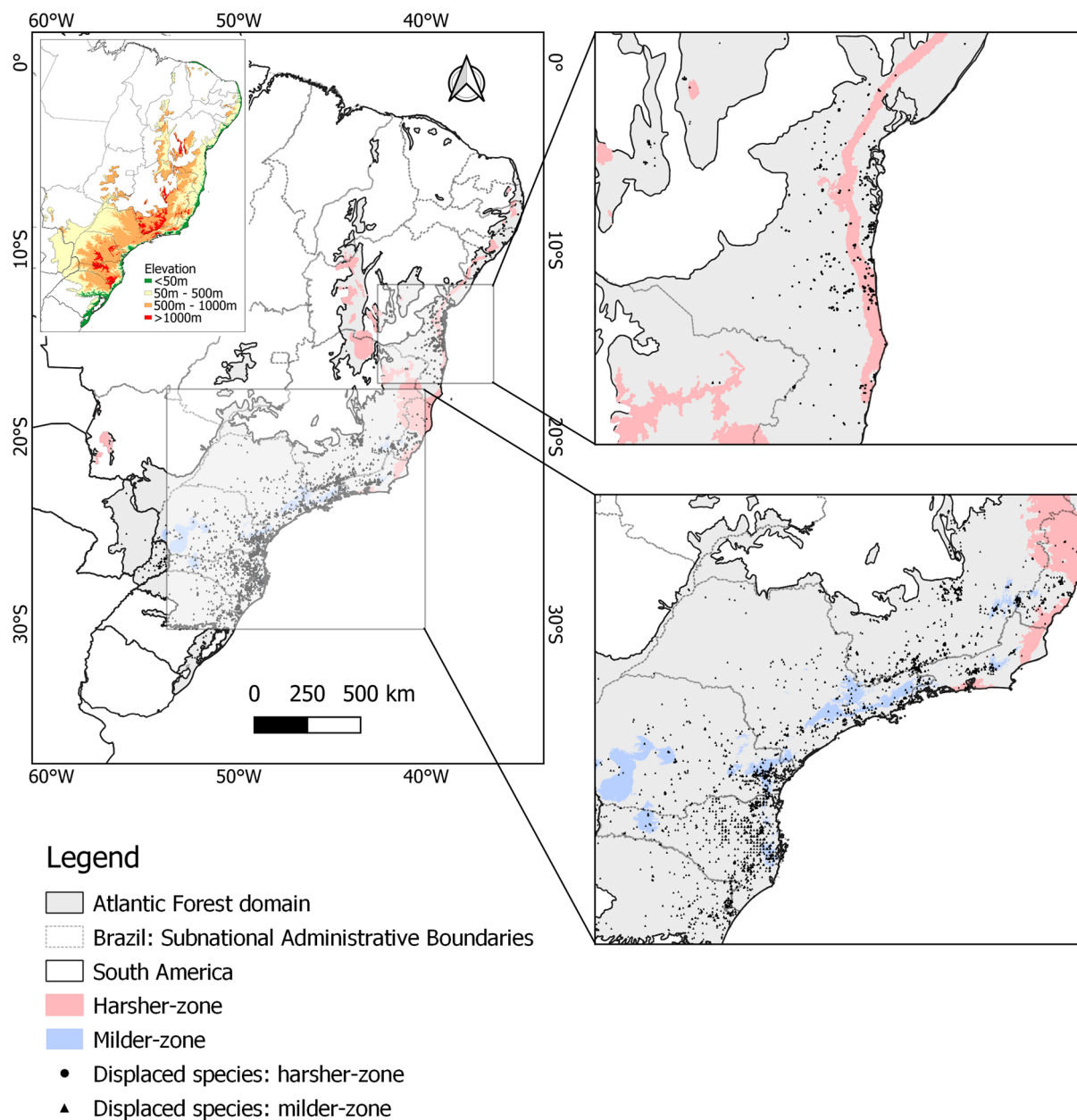
Fig. 5 Milder and harsher zones plotted from the intersection of the intervals calculated from the mean and standard deviation (e.g., $\bar{x}-s$; $\bar{x}+s$) of the PCA axes

compared to the optimistic predictions for the same zone (n = 222; 27% of the species within the milder zone).

Although the majority of species within the harsher zone (n = 324) show adaptations to high temperatures (e.g. they have CAM metabolism and high leaf water retention capacity), there was a subset of species (n = 36; 11%) that still were displaced under more optimistic scenarios. It is likely that despite being adapted to areas with high temperature, low humidity and strong seasonality, the species that are predicted to be displaced may live close to their current limit of their climate niche, making them more susceptible. This
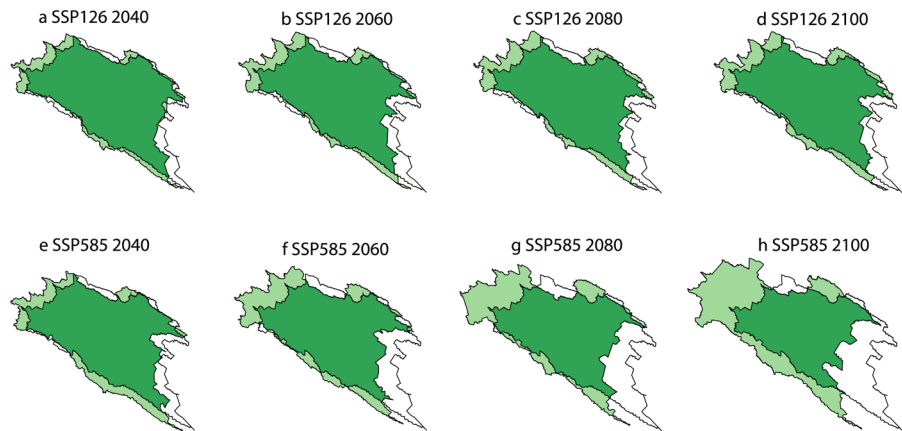
suggests that even subtle changes in environmental conditions may have important ecological consequences for some species (Reyes et al. 2021). The harsher zone corresponds geographically to the lowlands (304 ± 141 m asl.), mostly represented by deciduous and semideciduous seasonal forest; all the displaced species were species found in the northeastern coast such as the Bahia state. Many studies refer to a north/south division of the Atlantic Forest (Amorim and Pires 1996; Oliveira Filho and Fontes 2000; Pellegrino et al. 2005; Cabanne et al. 2007; Ledru et al. 2007; Thome et al. 2010; DaSilva and Pinto-da-Rocha 2011; DaSilva et al.

Table 3 Summary of displaced epiphyte species for each climate change scenario, according to major groups

Group	Present	Optimistic scenario (SSP126)			Pessimistic scenario (SSP585)		
		Displaced	Group (%)	Total (%)	Displaced	Group (%)	Total (%)
Bromeliaceae	404	46	11.39	3.02	77	19.06	5.06
Ferns and lycophytes	228	19	8.33	1.25	95	41.67	6.25
Orchidaceae	623	10	1.61	0.66	90	14.45	5.92
Other angiosperm families	266	11	4.14	0.72	42	15.79	2.76
Total	**1521**	**86**	**5.65**	**5.65**	**304**	**19.99**	**19.99**

Displacement was defined as any species that was outside the available climate space under a given projection and year. Present = number of recorded species used in the analysis; Displaced = number of displaced species; Group (%) = percentage of displaced species within each analysed group; Total (%) = percentage of displaced species of the total number of species

Fig. 6 Predicted consequences of climate space shifts according to different time frames and different climate change scenarios (**a**–**h**). The white area represents the current climate space, light green represents the future-predicted climate space, and dark green shows the overlap between current and predicted (see Table 4 for details)

a SSP126 2040 b SSP126 2060 c SSP126 2080 d SSP126 2100

e SSP585 2040 f SSP585 2060 g SSP585 2080 h SSP585 2100

2015). The Doce River valley in northern Espirito Santo represents the barrier responsible for this disjunction, which separated the north-eastern region of AF from the south-eastern and southern regions. Stable Pleistocene forest refuges were formed even during the driest periods of the Quaternary (during the last glacial maximum, about 21 thousand years ago) in Bahia (in the Central Corridor of AF, north of the Rio Doce valley) and Pernambuco (further North) (Carnaval and Moritz 2008). Currently, the "Bahia refuge" (Carnaval and Moritz 2008; de Mello Martins 2011) corresponds to the "Bahia endemism area", one of the five main endemism areas of the AF (Silva and Casteleti 2003). Nearly 80% of species displaced in the harsher zone are endemic to the Bahia region (Flora do Brasil 2020). For example, the genera *Aechmea* A. Juss. and *Lymania* R.W. Read had a particularly high number of endemic species that will be displaced (nine and six respectively), of which seven and five are endemic to the state.

The larger shift in the climate space predicted for the pessimistic scenario (up to 35%), is likely to affect species that occur in the milder zone. For example, we found that species in the milder zone occurred more frequently in higher elevation areas (693 m ± 227 m asl.) and areas with lower mean temperatures (18.5 °C ± 1.15 °C). Geographically, the milder zone corresponds to the mountain formations that spans from the southern Brazilian states to the south-eastern states of Espírito Santo and Minas Gerais, as well as the lower altitude areas in southern Brazil. This region encompasses a great variety of AF formations from submontana (50–500 m a.s.l.) to altomontana (> 1000 m a.s.l.) vegetation such as mixed ombrophilous forest, seasonal semideciduous forest and ombrophilous dense forest.

Ferns and lycophytes are likely to have the highest percentage of displaced species (e.g. n = 19–95; 8–42%). Other studies have found comparable results for epiphytic ferns. For example, Pie et al. (2022) found that 36–67 (28–53%) of epiphytic ferns and lycophytes in Honduras will be displaced by the year 2049–2099 under RCP2.6 and RCP8.5 projections respectively (IPCC 5th Assessment Report scenarios, 2014; RCP2.6 assumes that CO_2 emissions start declining by 2020 and go to zero by 2100; RCP8.5 assumes that emissions continue to rise throughout the twenty-first century). Similarly, Reyes-Chávez et al. (2021) found that over 47% of ferns and lycophytes species along the highest mountain in Celaque National Park, Honduras will have to shift their range fully or partially above the maximum elevation of the mountain. We found that species within the genera *Elaphoglossum* and *Hymenophyllum* will be the most affected under

Table 4 Predicted consequences of climate space shifts according to different climate change scenarios

Climatic space	Outside					Within					Total area	Overlap
	All	Bromeliads	Orchids	Ferns and Lycophytes	Other angiosperm families	All	Bromeliads	Orchids	Ferns and Lycophytes	Other angiosperm families		
Present	0	0	0	0	0	1521	404	623	228	266	100	100
SPP126 2040	11	8	1	0	0	1510	396	622	228	266	102.9	89.7
SPP126 2060	58	29	8	15	6	1463	375	615	213	260	100.5	84.8
SPP126 2080	64	37	7	12	8	1457	367	616	216	258	102.4	84.5
SPP126 2100	78	44	8	16	10	1443	360	615	212	256	103.3	84.5
SPP585 2040	43	22	4	13	4	1478	382	619	215	262	104.9	86.2
SPP585 2060	100	34	25	27	14	1421	370	598	201	252	101.8	78.1
SPP585 2080	138	38	30	55	15	1383	366	593	173	251	102.9	72.2
SPP585 2100	246	36	79	93	38	1275	368	544	135	228	112.8	65.6

Species counts correspond to the number of species whose mean climatic niche will lie inside or outside each climatic space. Total area (%) indicates the relative size of the climatic space in relation to the present, whereas the overlap indicates the relative area of overlap of the corresponding climatic space in relation to the present (see also Fig. 4)

the pessimistic scenario (SSP585) and that 19 and 13 species respectively, will be displaced by 2100. Within the AF, *Elaphoglossum* is especially diverse in mid-elevation montane forests, from 500 to 1500 m (Matos and Mickel 2014). *Hymenophyllum* on the other hand is highly hygrophilous, and is usually associated with microhabitats that are constantly humid (Kelly 1985; Hietz and Hietz-Seifert 1995), since their species lack cuticles (or have greatly reduced cuticles), differentiated epidermises, and stomata (Krömer et al. 2006). Particularly high diversity mountain regions (Suissa et al. 2021) that are occupied by species with narrow climate niches (e.g. many hygrophilous plants) (Pie et al. 2022), might be at greater risk. However, Kessler and Kluge (2022) recently suggested that the effect of climate change on ferns in mountain areas will be very species and context specific, as we currently still lack detailed data on how biotic and abiotic interacting effects might limit species responses to a changing climate.

For practical reasons of working with over 800 species in this study, we did not explicitly analyse intraspecific variation in climatic niches even though intraspecific variation in functional traits might play a relevant role in community dynamics (e.g., Lajoie and Vellend 2015; Niu et al. 2020; Kessler and Fluge 2022). Also, epiphytes are particularly sensitive to microclimatic changes (Hietz 1999), which are currently very difficult to account for in niche model simulations due to the lack of detailed spatial and temporal climate layers. One way this could be achieved is to use Climate Envelope Models (CEM) and parametrize them by using recent estimates of below canopy temperature and precipitation conditions, which account for the buffering potential of the above canopy (e.g. de Frenne et al. 2019; Zheng and Jia 2020). However, these models would be limited to individual species and would be computationally challenging to do across all AF epiphytes. Last, the epiphyte dataset we used may have collection biases, particularly for smaller, less-well surveyed epiphyte groups (see Araujo and Ramos 2021 for a detailed discussion). In addition, we calculated the average position that the climatic niche of each species occupies in relation to the predicted climatic space for the AF. Thus, it does not necessarily mean that species identified in our study to be displaced will disappear. However, it could increase the risk of extinction due to these species being closer to their climate niche limits, making them more vulnerable during perturbation events (e.g. droughts).

It is also important to highlight that, epiphytes are dependent on the host trees for their survival, thus any changes to the host tree cover or composition, due to climate and/or land-use change, could exacerbate our findings. For example, the AF has been significantly over-exploited in the past, including the cutting of brazilwood trees in the sixteenth century and later the removal of the forest cover for agricultural species such as sugarcane, coffee, cocoa,

and foraging crops (Tabarelli 2005; Ribeiro et al. 2011). It is also home to the biggest cities in Brazil (São Paulo, Rio de Janeiro, and Porto Alegre) and evidence suggest that many potential host trees for epiphytes might disappear and/or change their community structure due to rapid changes in climate (Colombo and Joly 2010; Pinho et al. 2021).

Conclusion

In conclusion, we found that the AF climate space is likely to shift by 10–35% by the year 2100. Almost 20% of epiphyte species will have their mean climatic niche displaced, many of which are ferns and bromeliads. However, the severity of species displacement differed within a geographical context, while the harsher zone seems to be more impacted than the milder zone under SSP126 projections. Furthermore, species displacement was ten times higher under SSP585 projections for the milder zone compared to other zones. The findings from this work are important, as they can directly translate into current and future conservation forest management planning. Epiphytes have a close ecological relationship with many trees, thus any changes in the assemblages of epiphyte host trees (e.g. as a result of forest strategies such as logging or restoration) could exacerbate the loss of epiphytes in the future. We recommend that the species climate niche space in considered when planning for conservation.

Declarations

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