





RESEARCH ARTICLE

The relative role of climate and biotic interactions in shaping the range limits of a neotropical orchid

Jacqueline Salvi de Mattos¹ | Fabio Pinheiro¹ | Bruno Garcia Luize¹  |
Cleber Juliano Neves Chaves¹ | Thales Moreira de Lima¹ | Clarisse Palma da Silva¹ |
Bárbara Simões Santos Leal^{1,2} 

¹Laboratory of Evolutionary Ecology and Plant Genomics, Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil

²Instituto Tecnológico Vale, Desenvolvimento Sustentável, Belém, Brazil

Correspondence

Fabio Pinheiro, Laboratory of Evolutionary Ecology and Plant Genomics, Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil.
Email: biopin@unicamp.br

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Abstract

Aim: The centre-periphery hypothesis (CPH) explains the decline of species abundance towards range limits and how this is driven by increasing ecological marginality. So far, most studies testing the CPH have focused on abiotic factors contributing to marginality, while the role of biotic interactions in limiting species distribution has been neglected. Here, we investigate both drivers' roles in restricting an orchid's range along a broad environmental gradient.

Location: Atlantic Forest and Pampas grasslands (south and southeastern Brazil).

Taxa: Sand dune orchid *Epidendrum fulgens* (Orchidaceae).

Methods: We integrated empirical data on geographical distribution, pollinator richness and genetic diversity along the entire range of the species to investigate whether range limits match niche limits and whether habitat suitability declines towards low- and high-latitude species ranges. We performed niche models to predict niche limits and used polynomial and linear regression models to investigate the associations between ecological niche and species range as well as to test the relationship between genetic-derived metrics and the geographical and ecological distances.

Results: Ecological conditions become more marginal towards the edges of the *E. fulgens* range, with an abrupt variation in precipitation. While pollinator richness increases habitat suitability of *E. fulgens* in the low-latitude edge range, climate has primarily shaped the species' high-latitude limit. Genetic diversity within populations decreases, while genetic differentiation increases towards both margins, although with a more consistent pattern for the low-latitude component.

Main Conclusions: This study corroborates the predictions of CPH regarding ecological and genetic patterns of variation in space and highlights distinct factors limiting geographical distribution at the opposite margins of a latitudinal and narrowly distributed species. This improves our understanding on how biotic and abiotic variables limit species distribution ranges along latitudinal gradients in an extremely diverse and vulnerable tropical ecosystem, with potential for informing conservation practices.

KEYWORDS

biogeography, Brazilian Atlantic Forest, ecological modelling, genetic diversity, niche suitability, range edges, restingas

1 | INTRODUCTION

The study of species' geographic ranges and how ecological and genetic processes influence them is of great importance in ecology and evolutionary biology (Lee-Yaw et al., 2017; Willi & Van Buskirk, 2019), and the understanding of how these processes act on biodiversity distribution can aid predicting species responses to ongoing climatic changes (Sexton et al., 2009). The 'centre-periphery hypothesis' (CPH; also referred to as 'abundant centre hypothesis', Gaston, 2009; Lee-Yaw et al., 2017; Pironon et al., 2017) is one of the proposed models to explain ecological, genetic and demographic variations along species distributions (Eckert et al., 2008; Gaston, 2009; Pironon et al., 2017). Such hypothesis assumes that species distribution is a geographical representation of its ecological niche (Hutchinson, 1957). Thus, the highest population densities and individuals' abundance would occur in the centre of their geographical distribution (Brown, 1984) and decline towards the periphery. Consequently, the increased ecological marginality and the higher isolation among populations towards the edges of the species range would lead to decreased genetic diversity within populations and increased inbreeding levels and genetic differentiation between populations (Eckert et al., 2008; Lee-Yaw et al., 2017; Pironon et al., 2017).

Despite the great influence of the CPH on ecology and evolution, the evidence for such a pattern is sparse across taxa (Dallas et al., 2017; Pironon et al., 2017). Indeed, a recent meta-analysis showed a decline in population abundance towards the periphery of the distribution for many animals and plants (Pironon et al., 2017), but exceptions to this pattern have also been extensively demonstrated in the literature (e.g. Sagarin et al., 2006; Sexton et al., 2009). With the increasing number of studies contradicting the CPH expectations, it has been proposed that this should only be a valid hypothesis for some groups of organisms or in particular scales or biogeographical areas (Eckert et al., 2008; Freitas, 2022; Pironon et al., 2017). In addition, it has been proposed that the ecological niche centre (or the environmental space centre) plays a critical role in defining population abundance (abundant-niche-centre hypothesis, Martínez-Meyer et al., 2013, Osorio-Olvera et al., 2020). This concept has gained more acceptance in the last decade, as recent studies have shown that standing genetic variation should be higher in niche-central populations (Lira-Noriega & Manthey, 2014). Nevertheless, both abundance-centre (i.e. CPH) and abundance-niche-centre hypotheses have received mixed evidence, probably due to differences in sampling and methodology (Brown, 1984; Dallas & Hastings, 2018; Dallas & Santini, 2020; Dallas et al., 2017). Evidence from simulated data also suggests that both hypotheses might not even be mutually exclusive when accounting for dispersal ability and the environmental set-up of the species in focus (Feng & Qiao, 2022).

Species range limits, that is, the expression of a species' ecological niche in space (Sexton et al., 2009), are often difficult to define due to the variety of factors involved (i.e. biotic interactions, abiotic conditions, dispersal and demographic history; Sagarin

et al., 2006) and the complexity of their interactions. Despite increasing evidence of the importance of biotic interactions in species distributions (Papuga et al., 2018), most studies testing the CPH have relied solely on the role of climatic factors (Diniz-Filho et al., 2009; Lee-Yaw et al., 2017; Lira-Noriega & Manthey, 2014; Pironon et al., 2015). For plants, recent studies have demonstrated that biotic interactions and dispersal ability might be equally or even more important than climatic drivers in defining distribution limits and determining potential range shifts in climatic change scenarios (Brown & Vellend, 2014; Neuschulz et al., 2018). Therefore, including parameters underlying plant reproduction, such as abundance and/or pollinators' richness, may add an important nuance to the distribution patterns of plants (Moeller et al., 2012; Morris et al., 2007; Sánchez-Castro et al., 2022). Although pollinator abundance tightly determines interaction frequency (Sahli & Conner, 2006; Vázquez et al., 2005), pollinator richness has also been demonstrated to be an essential factor underlying plant reproductive success (Albrecht et al., 2012; Winfree et al., 2018). The lack of potential pollinators (as defined by abundance and richness components) at the range margins may explain the lower plant abundance at range margins (Gaston, 2009). Indeed, such pattern at range edges is predicted by the CPH to be strongly associated with lower genetic diversity and higher levels of inbreeding, but empirical evidence of such associations is still scarce (but see Chalcoff et al., 2011; Moeller et al., 2012; Sánchez-Castro et al., 2022; Stone & Jenkins, 2007).

Here, we investigate the potential biotic and abiotic drivers of the distribution of *Epidendrum fulgens* Brogn., a perennial orchid pollinated by deceit by a diverse array of butterfly species (Fuhro et al., 2010). *Epidendrum fulgens* occurs in a North-South oriented distribution along the southeastern coast of the Brazilian Atlantic Forest (BAF), in the *restinga* (sand dune) vegetation, and on the southern granitic rocky outcrops within the Brazilian Pampas grasslands (Pinheiro et al., 2011; Figure 1). We integrated empirical data on geographical distribution, genetic diversity and structure (previously generated by Pinheiro et al., 2011) of *E. fulgens* and pollinator richness data to investigate the factors limiting the species' linear distribution along the Brazilian Atlantic coast. For this, we formulated four main questions: (1) Do geographical range limits match the niche limits of the species? (2) Are the environmental conditions changing at the species' low- and high-latitude range margins?; (3) Does genetic diversity decrease and genetic structure and inbreeding increase from central to peripheral distribution, as predicted by the CPH? and (4) May the lack of potential pollinators help to explain low- and high-latitude limits of the species distribution? Understanding the abiotic and biotic processes that drive species' range limits is a fundamental question in ecology with practical implications for species conservation (Willi & Van Buskirk, 2019). By gathering information on the genetic variation and niche suitability of this latitudinal and narrowly distributed neotropical orchid, we hope to elucidate the knowledge gap of the causes of range limitations and niche restrictions in such extremely diverse and vulnerable tropical ecosystems.

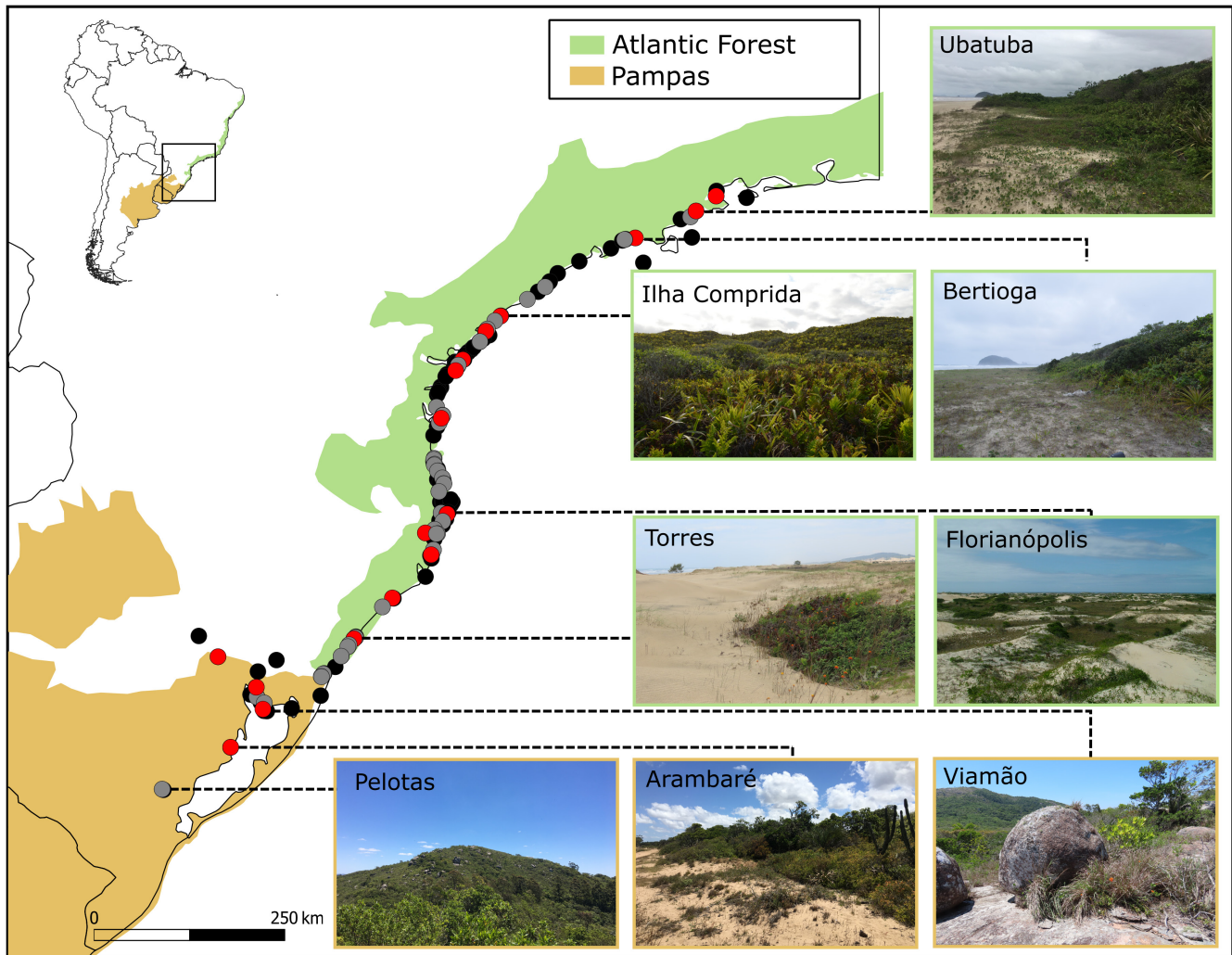


FIGURE 1 Geographical distribution along the southeastern coast of Brazil and habitat variation of *Epidendrum fulgens* (Orchidaceae). The subset of 40 of 212 records employed in the ecological niche models is highlighted in grey, while the 16 localities sampled for genetic analyses in Pinheiro et al. (2011) are in red. The remaining records are plotted in black. The Atlantic Forest (green) and Pampas grasslands (yellow) provinces are delimited according to Morrone's (2014) biogeographical regionalization of the Neotropical region. Map is plotted in Mercator projection.

2 | MATERIALS AND METHODS

2.1 | Study system

Epidendrum fulgens is a common terrestrial orchid found on sand dune vegetation of Southern and Southeastern Brazil (Figure 1). It belongs to the *Amphyglottium* subgenus, a group of species with ecological preferences for harsh environments (Pinheiro & Cozzolino, 2013). This is the *Epidendrum* with the Southernmost range (Hågsater & Soto Arenas, 2005) and is found growing directly on sandy or rocky outcrops. To date, 22 butterfly species have been identified as pollinators of *E. fulgens* (Fuhro et al., 2010; Pansarin & Amaral, 2008), being the only group identified as such. *Epidendrum fulgens* do not offer any reward for pollinators, characterizing a food-deceptive pollination system (Cardoso-Gustavson et al., 2018). Although self-compatible, the fruit set strongly depends on pollinator visits (Fuhro

et al., 2010). Butterflies are also responsible for the high levels of pollen movement detected within (Sujii et al., 2019) and among populations (Pinheiro et al., 2011). In fact, gene exchange via pollen in *E. fulgens* is more than tenfold greater than that via seeds (Pinheiro et al., 2011), increasing the importance of pollination services for reproductive success. Given the importance of pollinators for fruit set and pollen movement, we expect that *E. fulgens* persistence is influenced by pollinators presence.

2.2 | Estimation of the geographical range

We compiled occurrence records of *E. fulgens* from the Global Biodiversity Information Facility (GBIF; <http://gbif.org>) and SpLink (<http://specieslink.net>) online databases and from extensive fieldwork during the last 15 years by our research group. We used exact

or approximate coordinates obtained from such databases if they contain a field collector description. In the last case, we assigned a new geographical coordinate based on geographic gazetteers considering the very narrow kind of habitat that the species occupy. After filtering out redundant coordinates, we retained a total of 212 georeferenced records for the species (Figure 1).

To estimate species' geographic range limits, we used the occurrence records of *E. fulgens* to fit convex and alpha hulls (AH) using the 'conR' package (Dauby et al., 2017) implemented in R (R Core Team, 2017). Convex hull (CH) is defined as the minimum convex polygon (MCP) encompassing all observed occurrences by joining the outermost species' records (Figure S1). In turn, AH apply the parameter alpha to create concavities on the MCP. To fit the AH, the parameter alpha was settled to 1 and 3 (AH1 and AH3, Figure S1), higher alpha means polygons with higher concavities, based on the algorithm by Edelsbrunner et al. (1983). We defined the centre of the species' geographic range as the average of the centroids measured for the three polygons characterizing the species range (CH, AH1 and AH3, Figure S1; Figure 2).

2.3 | Estimation of the ecological niche

We modelled the ecological niche of *E. fulgens* using the Maximum Entropy (MAXENT) approach based on the subset of 40 occurrence records with original and precise coordinates previously thinned in a radius of 9 km (Figure 1, see Appendix S1 for detailed filtering procedures). Using the framework of van Proosdij et al. (2016), we confirmed that these 40 records are enough to avoid any severe shortfalls caused solely by the low number of presence points (see Appendix S1). As abiotic predictors of the ENMs, we extracted 19 bioclimatic variables at 30 arc seconds of resolution (ca. 1 km) from the CHELSA database (Karger et al., 2017) and downloaded SRTM elevation data from the WorldClim database (Fick & Hijmans, 2017). For modelling, we retrieved the following predictor variables based on a maximum of 0.7 of correlation: Annual Mean Temperature (Bio 1), Temperature Seasonality (Bio 4), Mean Temperature of Coldest Quarter (Bio 11), Precipitation of Wettest Month (Bio 13), Precipitation of Driest Quarter (Bio 17), Precipitation of Warmest Quarter (Bio 18) and Precipitation of Coldest Quarter (Bio 19). We cropped such bioclimatic layers by tracing a one-degree buffer area around the CH polygon created from the full set of occurrence records.

For modelling, we replicated 10 MAXENT runs with randomly selected background points using the default settings of the 'biomod2' R package (Thuiller et al., 2016), except for maximum iterations, which were set to 10,000. Ten distinct sets of background points were generated per replicated run to avoid potential bias, totalling 100 individual models. For each model, we split the observation dataset into 70% of data for training and 30% for testing and used the area under the receiver operating characteristic (ROC) curve (AUC) and the true skill statistics (TSS; Allouche et al., 2006) for evaluation. We further used an ensemble approach to combine

predictive outputs weighted by the TSS value of each model, as implemented in 'biomod2'. For the final consensus, we retained models with $TSS > 0.4$ and $AUC > 0.7$. The threshold that returned the highest TSS score was used to convert continuous predicted probabilities into a binomial output. The importance of each bioclimatic variable to the models was averaged over 100 permutations.

2.4 | Associations between ecological niche and species range

To assess the changes in the environmental conditions at the species' geographic range limits, we compared the values of the two environmental predictors that contributed most to the ENM fitting (i.e. Precipitation of Wettest Month and Precipitation of Warmest Quarter, see Results) from the centre to the low- and high-latitude peripheries of *E. fulgens* distribution. For this, we employed 4th-degree polynomial models, including values of both variables extracted from all cells within and outside the MCP (considering the latitude and longitude limits of the MCP) against their distance from the average among computed centroids of MCPs (CH, AH1 and AH3).

To test whether the species niche becomes more marginal at the low- and high-latitude range periphery, we evaluated the association between the distance to the species' geographic range centre and the distance to the species' niche centre using linear models. The species' niche was characterized as the environmental space built from the seven bioclimatic variables used in the ENMs. For this, we extracted the cell values of the bioclimatic raster for each occurrence record and performed a PCA to summarize data dimensionality (Figure S2). The first two axes of the PCA explained 99.1% of the bioclimatic variation, with the first component more related to Temperature Seasonality (0.915) and the second to Precipitation of the Warmest Quarter (0.871). The first two PCA axes were then applied to compute the CH that defines the species' environmental niche space and the niche centre (i.e. the centroid of this niche space, Figure S2). We estimated niche marginality as the Euclidean distance of predicted PCs (PC1 and PC2) values for each occurrence record and the niche centre. Higher distances to the species' niche centre mean that a species' range locality has more disparate environmental conditions. Using linear models, we also tested whether habitat suitability (as predicted by the ENM) decreases as far away the species are from the geographic range centre at both low and high latitude. All analyses were implemented using the package 'stats' in the R environment.

2.5 | Influence of geographical and ecological distances on genetic variation

To calculate genetic diversity and differentiation indexes for *E. fulgens*, we used information from individual genotypes previously obtained from nine nuclear microsatellite markers genotyped in 424

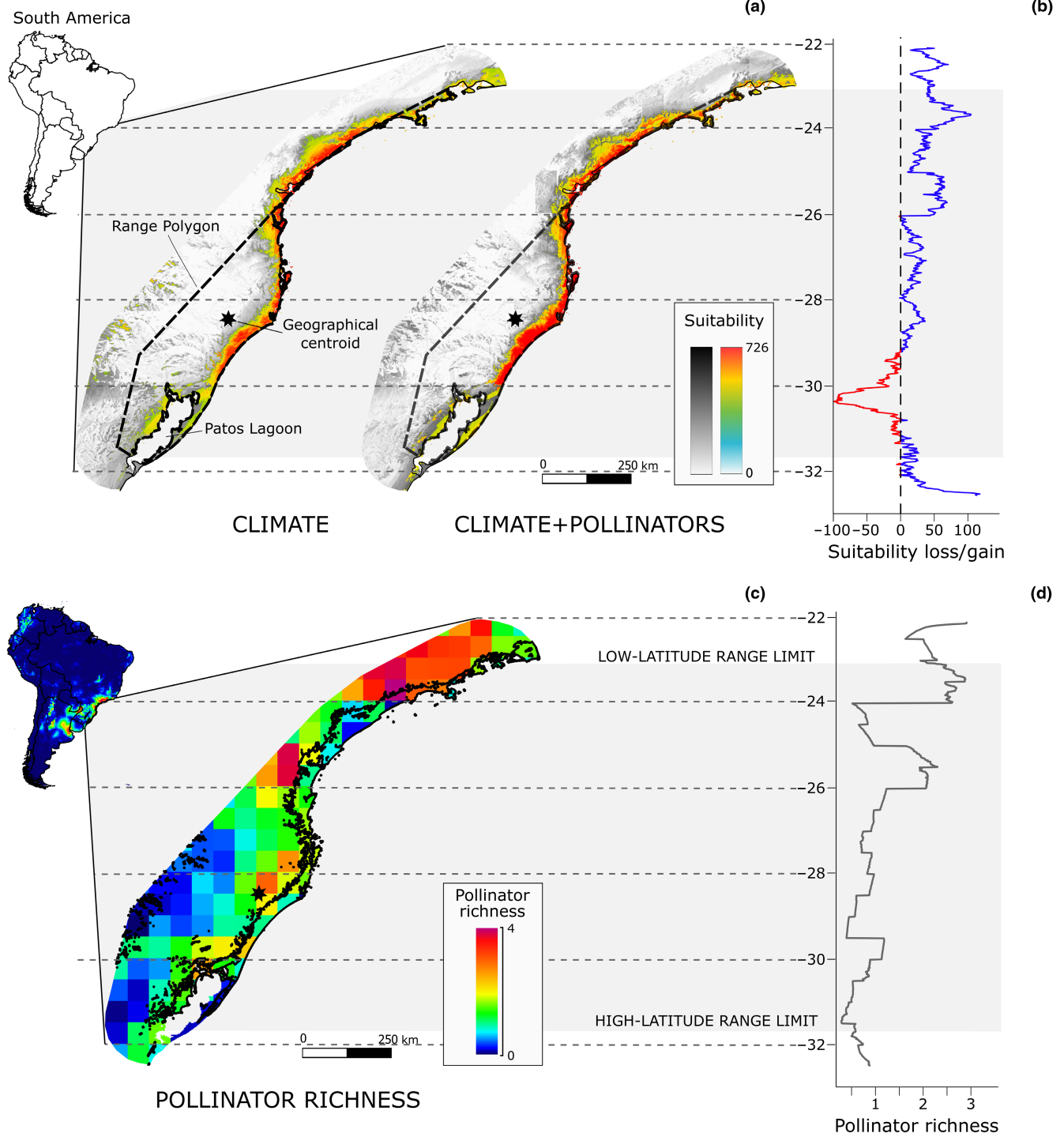


FIGURE 2 Comparisons between geographical range and niche limits of *Epidendrum fulgens* and variation in pollinator richness across *E. fulgens* distribution area along the southeastern coast of Brazil. The geographical range of *E. fulgens*, as defined by the CH RP, is shown as a dashed black line, while the geographical centroid, as defined by the average among computed CH, AH1 and AH3 centroids, is shown as a black star. The known geographical limits of *E. fulgens*, as defined by CH, are delimited by the grey area. Predicted suitable areas for *Epidendrum fulgens*, as inferred by the maximum entropy (MAXENT) method based on seven bioclimatic variables or seven bioclimatic variables plus pollinator richness, are shown in (a). Predicted areas above the threshold for which true skill statistics achieved the highest score are shown in colours, while areas below such threshold are shown in black and white for both ensemble models. The average gain (blue) or loss (red) in suitability per latitude after the inclusion of the pollinator richness as a predictor of the model is shown in (b). The interpolation of *Epidendrum fulgens* pollinator richness is shown in (c), while the average pollinator richness per latitude, according to the interpolation analysis, is shown in (d). Maps are plotted in Mercator projection.

individuals from 16 populations found along the entire range of *E. fulgens* (Pinheiro et al., 2011; see Figure 1). To evaluate the genetic patterns along with the species' range, we used two different diversity indexes: expected heterozygosity (H_E) and allele richness (A_R) per population, as calculated with FSTAT 2.9.3.2 (Goudet, 1995) and MSA 4.05 (Dieringer & Schlotterer, 2003) and also the inbreeding coefficient (F_{IS} ; Weir & Cockerham, 1984). We also accounted for the genetic differentiation between populations by calculating the population-specific F_{ST} (Weir & Hill, 2002) in the software ARLEQUIN 3.0 (Excoffier et al., 2005).

To test if central populations indeed present higher genetic diversity and smaller genetic differentiation as presumed by the CPH, we conducted linear regression models using the genetic variation and inbreeding coefficient values (H_E , A_R , F_{IS}) and genetic differentiation parameters (population-specific F_{ST}) as the response variables, and the logarithm of the distance of each population from the geographic range centre (km) and from the species' environmental niche centre (environmental distance unitless) as the explanatory variables. To explore the genetic diversity and structure variation towards both low- and high-latitude limits, we conducted the linear regressions separately for low-latitude and high-latitude distribution (i.e. above and below the species geographic centroid). We then partitioned the variance of each model using the package 'relaimpo' (Grömping, 2006) to test which would better explain the variation in genetic diversity and structure along with the species distribution. All the regressions were generated using the 'lm' function of the package 'stats' in the R environment (R Core Team, 2017).

2.6 | Influence of pollinators on the geographical range and ecological niche

To investigate whether the current distribution of *E. fulgens* is constrained by the richness of pollinators, we first gathered the occurrence records of 17 butterfly species previously identified at the species level as flower visitors and potential pollinators of *E. fulgens* by Fuhro et al. (2010) from GBIF (<http://gbif.org>) and iNaturalist databases (<https://www.inaturalist.org>). For this, we employed automatic functions to import the occurrence records from both online datasets using the 'rgbif' and 'rinat' R-packages (Barve & Hart, 2021; Chamberlain et al., 2022) and then excluded the redundant or inaccurate records using the 'CoordinateCleaner' R-package (Zizka et al., 2019). We removed three out of 17 species with less than 14 occurrence records. The remaining species' final number of records varied from 42 to 425 (Figure S3).

To test the effect of pollinator richness on *E. fulgens* distribution, we first produced a 15' cells raster to group all gathered occurrence records of pollinator species using the 'raster' R-package (Hijmans, 2021). This raster was then interpolated according to a model that fit the local species richness to a thin plate spline regression using the four first components of the PCA bioclimatic summarization as independent variables, using the 'raster' and 'fields' R-packages (Hijmans, 2021; Nychka et al., 2021). Finally, we

repeated the modelling procedures described above but added the interpolated pollinator richness as a predictor of *E. fulgens* ecological niche at the exact resolution and extension of the seven bioclimatic variables. The performance of both ensembled ENMs—the one based only on the climate and the one based on climate plus pollinator richness—was then compared by estimating the differences in the *E. fulgens* suitability per latitude.

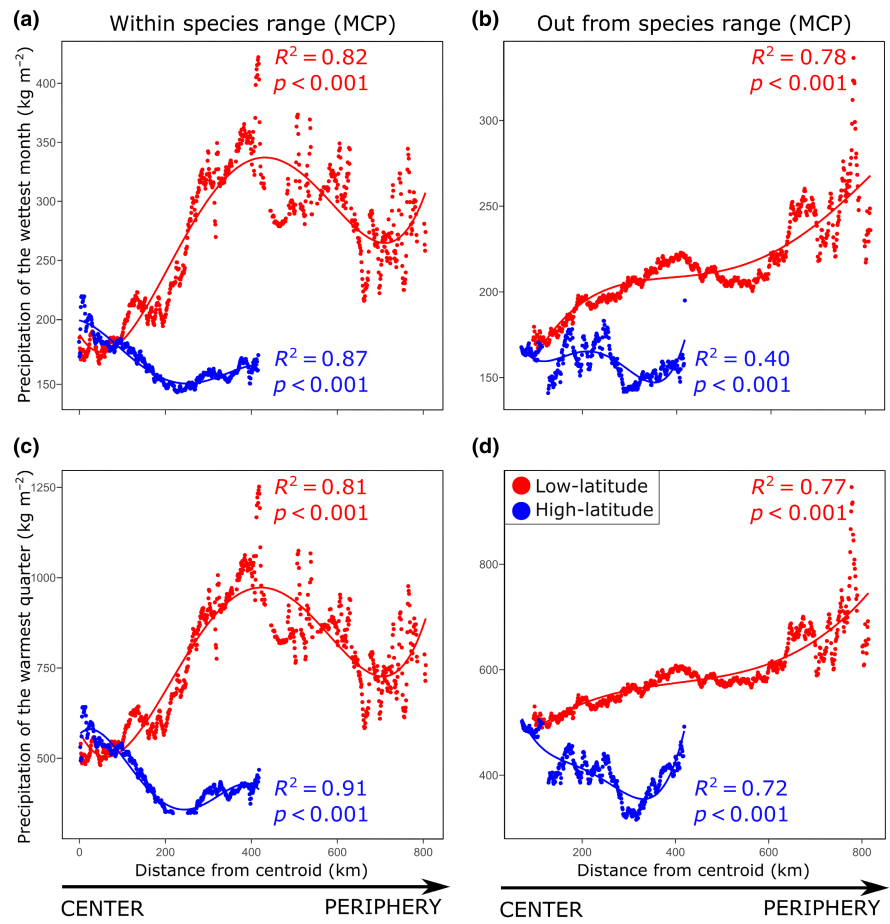
3 | RESULTS

3.1 | Associations between ecological niche and species range

The CH range polygon (RP) defined the geographic distribution of *E. fulgens* as a very narrow area at the low-latitude margin but a larger area at the high-latitude portion (Figure 2a), reflecting the few occurrences of *E. fulgens* found inland near the inner margin of Patos Lagoon (see Figure 1). The species' geographic range centre, by consequence, was displaced towards the high-latitude limits (Figure 2a). The ensembled ENM based on bioclimatic variables, in turn, only predicted areas along the Atlantic coast as highly suitable habitats for *E. fulgens*, except for the narrow area located east of the Patos Lagoon (southern Brazil), where the species has never been found (Figures 1 and 2a). As expected, the model showed that most inland areas are not suitable for the species but pointed to small, isolated tiny areas of low to moderate suitability in the southwestern region, far from known locations for the species (Figure 2a). At the low-latitude range edge, the suitable habitat revealed by ENM results extended beyond the species' range limits defined by the MCP (Figure 2a; Figure S1). A different pattern is observed in the high-latitude periphery, where the modelled suitable habitats along the seashore are linked to the RP limits. Precipitation of the warmest quarter and precipitation of the wettest month were the most critical variables for the ENM, with ca. 36% of the contribution, respectively (Figure S4a). The mean AUC and TSS were 0.817 (ranging from 0.7 to 0.95) and 0.635 (ranging from 0.4 to 0.9) for the ensembled ENM, respectively.

The two bioclimatic variables that most contributed to the niche models (precipitation of the wettest month and precipitation of the warmest quarter) show abrupt variations between 200–400km and 100–200km away from the geographical centre of *E. fulgens* range (i.e. the RP) towards the low- and high-latitude margins, respectively (Figure 3a,b). However, we observed much higher variances towards the low-latitude (variance of 2643.6 and 20,334.8 in both variables) than towards the high-latitude margins (variance of 706.2 and 9380.1 in both variables; Figure 3a,b). However, variability is smoother and gradual outside the species range, particularly towards the low-latitude limit (Figure 3c,d). Ecological niche conditions, as defined by climatic variables, did become more marginal towards the edges of the species' geographical range (Figure 4a—black line, $R^2=0.475$, $p<0.001$, $b_{std}=0.69$), deteriorating at similar rates towards the low- ($R^2=0.904$, $p<0.001$, $\beta_{std}=0.95$) and high-latitude

FIGURE 3 Changes in precipitation of the wettest month (a, b) and precipitation of the warmest quarter (c, d) from the centroid to the low (in red)- and high-latitude (in blue) range peripheries of *Epidendrum fulgens* and out of the geographic range of the species. Curves indicate 4th-order polynomial relationships.



($R^2=0.895$, $p<0.001$, $\beta_{std}=0.94$) range limits of *E. fulgens*. However, populations at the high-latitude limits are established in more marginal ecological niche conditions than populations in the low-latitude limits (Figure 4a). Conversely, estimated habitat suitability (according to Maxent) did not show any trend towards the limits of *E. fulgens* range ($R^2=0$, $p=0.50$, $\beta_{std}=0$; Figure 4b—black line). Whereas when evaluated separately, the habitat suitability shows a decreasing trend towards the range limits, which is more pronounced for the high- ($R^2=0.31$, $p<0.001$, $\beta_{std}=-0.57$) than for the low-latitude ($R^2=0.19$, $p<0.001$, $\beta_{std}=-0.45$) range limits of the species (Figure 4b). Also, habitat suitability is low for high latitude compared with the low-latitude populations (Figure 4b).

3.2 | Influence of geographical and environmental distances on genetic variation

The linear models, including environmental and geographical distances as predictors, indicated similar patterns of genetic diversity decrease towards high- and low-latitude margins, although with a more robust and significant change for the low-latitude component (Figure 5). For the low-latitude variation, we found significant decreases in allelic richness ($R^2=0.877$, $p<0.001$, $\beta=-1.94$ [geographical distance] and $\beta=-0.001$ [environmental distance]) and expected heterozygosity ($R^2=0.75$, $p=0.003$, $\beta=-1.9e+02$

[geographical distance] and $\beta=4.7e-03$ [environmental distance]) as farther away from the centre of distribution (Figure 5a,b). Models explained 90.49% (environmental distance=44.4% and geographical distance=46%) and 80.55% (environmental distance=36.7%, geographical distance=43.8%) of allelic richness and expected heterozygosity variances for the low-latitude populations, respectively. For the high-latitude populations, we found no significant tendency of decreasing allelic richness ($R^2=0.74$, $p=0.2$, $\beta=-0.757$ [geographical distance] and $\beta=-0.001$ [environmental distance]) and expected heterozygosity ($R^2=0.46$, $p=0.12$, $\beta=93.906$ [geographical distance] and $\beta=-0.103$ [environmental distance]). Models explained a total of 82.77% (environmental distance=46.6% and geographical distance=36.15%) and 64.2% (environmental distance=46.8%, geographical distance=17.3%), respectively.

The inbreeding coefficient increased slightly, although not significantly, towards both low-latitude ($R^2=-0.145$, $p=0.66$, $\beta=-0.127$ [geographical distance] and $\beta=3.1e-05$ [environmental distance]) and high-latitude edges ($R^2=-0.407$, $p=0.88$, $\beta=-1.2e-01$ [geographical distance] and $\beta=8.3e-05$ [environmental distance]). Nevertheless, models explained only 10.87% of the variance (geographical distance=3.9%, environmental distance=6.9%) for the low-latitude and 6.15% (geographical distance=1.9%, environmental distance=4.17%) for the high-latitude locations.

The genetic differentiation among populations (i.e. population-specific F_{ST}), in turn, significantly increased with both predictors

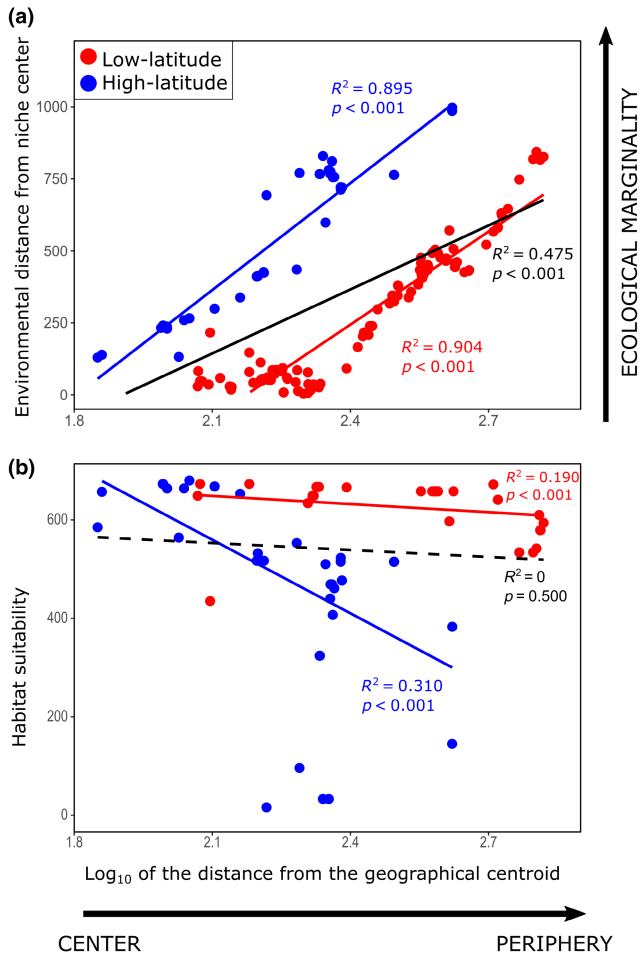


FIGURE 4 The association between the distance to the geographic low (red)- and high-latitude (blue) range peripheries and the distance to the environmental niche centroid (a) or to the habitat suitability as predicted from the ecological niche model of *Epidendrum fulgens* (b).

($R^2=0.725$, $p=0.005$, $\beta=1.7e-02$ [geographical distance] and $\beta=-2.4e-06$ [environmental distance]; Figure 5c) towards the low-latitude margin, with 78.65% of the variance being explained by the model (environmental distance=34.82%, geographical distance =43.81%). On the other hand, we did not recover a significant increase towards the high-latitude edge ($R^2=0.327$, $p=0.2$, $\beta=-6.9e-03$ [geographical distance] and $\beta=5.4e-06$ [environmental distance]; Figure 5c), with 55.19% of the total variance being explained by the model (environmental distance=39.45%, geographical distance=15.73%).

3.3 | Influence of pollinators on the geographical range and ecological niche

The interpolation of pollinator richness indicated Southeastern Brazil as one of the most species-rich regions (Figure 2c). Within the *E. fulgens* distribution area (Figure 2c,d), the low-latitude portion shows the highest pollinator richness, whereas the isolated inland

areas in the high-latitude distribution of *E. fulgens* show the lowest pollinator richness (Figure 2c,d). The *E. fulgens* niche model, including the interpolated pollinator richness as a predictor, showed higher performance than the model with only bioclimatic variables (AUC and TSS evaluation metrics improved by 0.138 and 0.173, respectively). Precipitation of the warmest quarter and precipitation of the wettest month were again the most important variables for the model, with ca. 43% and 41% of the contribution, respectively, while pollinator richness showed a moderate contribution for the model (ca. 10%; Figure S4b). The model resulting from the inclusion of pollinator richness as a predictor for *E. fulgens* distribution projected similar range distribution for the species (Figure 2a) with increased suitability for the species at most latitudes, particularly at the low-latitude margin, in comparison with the previous model (Figure 2b). Notably, this model did not recover any suitable area for the species in the south (inland areas), resulting in a significant suitability loss close to -30° of latitude (Figure 2b).

4 | DISCUSSION

Our results show that ecological niche conditions become more marginal towards the edges of the *Epidendrum fulgens* range, with abrupt variation in environmental conditions towards high- and low-latitude range limits. Indeed, a marked loss of habitat suitability was detected at both high- and low-latitude range edges. The high-latitude range limits were well predicted by our niche models, suggesting that the climate restricts the southern spreading of the species. In contrast, our niche models did not predict the low-latitude range limits extending further from the current edges. The model using pollinator richness data shows increased habitat suitability mainly at the low-latitude range edge, which indicates that mutualistic interaction likely influences species persistence at this periphery. Our results also show that genetic diversity was negatively correlated to the distance from the geographic and environmental niche centres towards the low-latitude range edge, indicating population-level constraints at this region, such as reduced adaptive potential. Taken together, these results support the CPH and shed light on the role of biotic and abiotic factors on differently shaping low-latitude and high-latitude range edges of *E. fulgens*.

4.1 | Mismatches between distribution range and climatic niche limits

We found contrasting patterns in the low- and high-latitude margins of *E. fulgens* distribution, which is consistent with previous evidence on different factors shaping the demography and genetic patterns in both range limits for species occurring along coastal vegetation communities (Darling et al., 2008; Herlihy & Eckert, 2005) and organisms in general (Paquette & Hargreaves, 2021; Willi & Van Buskirk, 2022). While a match between climatic niche and geographic limits was observed in the high-latitude range edge of *E. fulgens*, suitable habitats

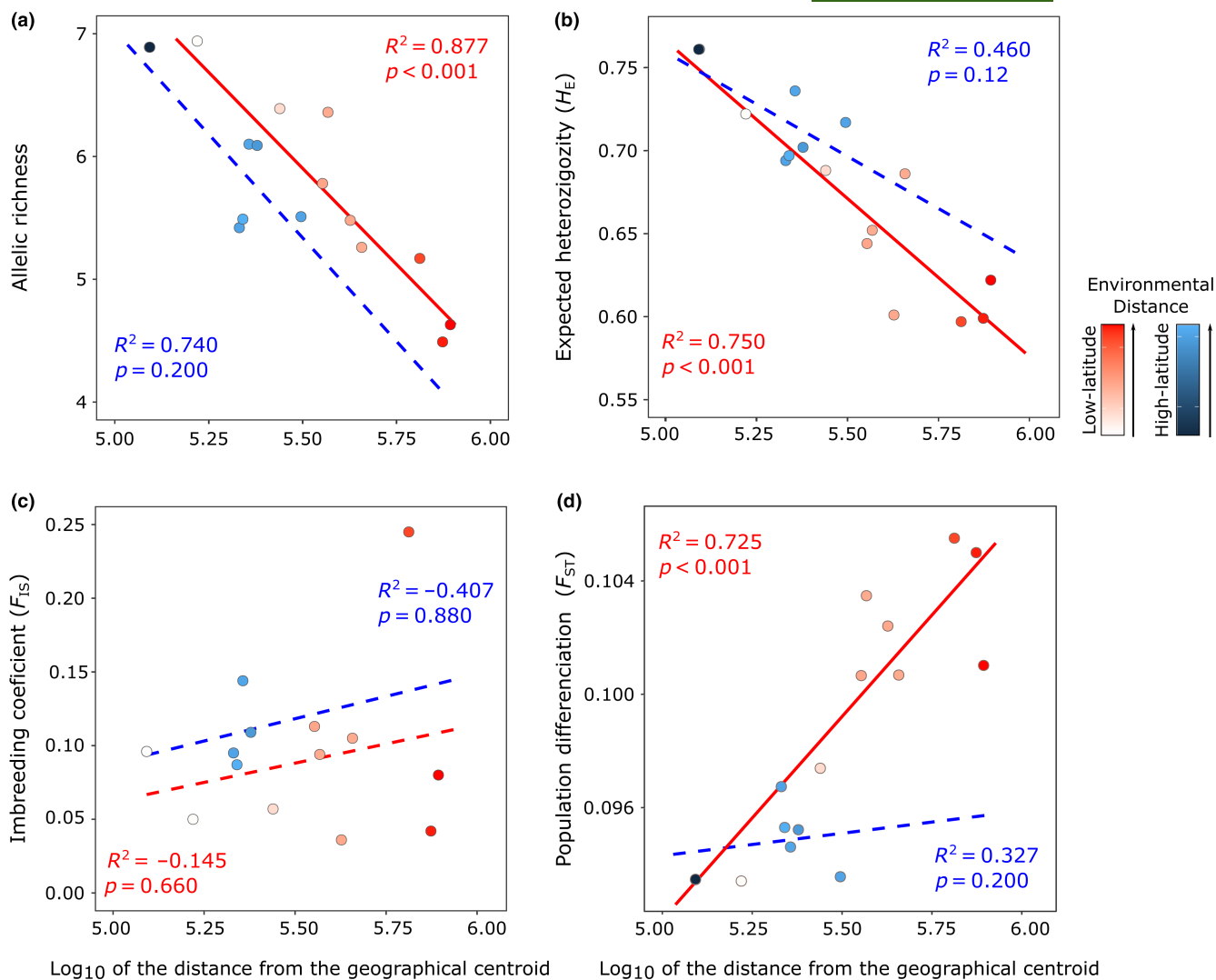


FIGURE 5 Relationships between allelic richness (a), expected heterozygosity (H_E ; b), inbreeding coefficient (F_{IS} ; c) and population-specific genetic differentiation (F_{ST} ; d) and the logarithm of the distances from the geographical (x-axis) and ecological niche centroid (gradient of colours) for the low- (red) and high-latitude (blue) populations of *Epidendrum fulgens*.

projected by models go beyond the low-latitude distribution range (Figure 2). Because the modelled climatic niche (as inferred from MAXENT) does not correspond with the fundamental niche of the species, we cannot exclude that other factors, including biotic ones, have also contributed to the match between distribution range and climatic niche limits. Differential patterns between species' warm and cold range edges were recognized by several authors throughout history (Darwin, 1859; MacArthur, 1984) and are based on the hypothesis that environmental conditions are more important in restricting species ranges at higher latitudes, while biotic interactions may prevail at lower latitudes. Recent reviews have found support for this hypothesis (Hargreaves et al., 2014; Paquette & Hargreaves, 2021), suggesting biotic interactions consistently influence species ranges at warm range edges, where biodiversity levels tend to increase as well as biotic interactions per se (Vamosi et al., 2006; Zvereva & Kozlov, 2021). In plants, negative interactions such as herbivory may impose severe restrictions on species distribution (Hargreaves

et al., 2018; Schemske et al., 2009), while mutualisms are expected to increase the distribution ranges (Afkhani et al., 2014). When mutualistic interactions decline towards warm range edges, such as pollinator activity (Sánchez-Castro et al., 2022), restrictions to range distribution may, thus, appear.

4.2 | Biotic and abiotic roles in shaping the range limits

The two most critical environmental variables contributing to niche models (Figure 3) are associated with precipitation, which may be interpreted as a limiting condition because low levels of humidity are retained by the coastal dunes across the entire range and also by rocky soils where *E. fulgens* occur in its high-latitude distribution (Figure 1). Abrupt changes in these bioclimatic variables are found from close to the centre of distribution of this species towards the

geographic range edges (Figure 3), suggesting a worsening of environmental conditions, with a faster deterioration towards the high-latitude limits. Beyond the species range edge, the same variables show a smooth variation, contrasting with the pattern observed within the species range (Figure 3). In fact, *E. fulgens* is the southernmost species within the genus, which show higher levels of diversity in the Andean Tropical region (Hågsater & Soto Arenas, 2005), suggesting environmental conditions severely affect the distribution of the genus as a whole. Climatic niche models also projected suitable areas along the eastern margin of Patos Lagoon (Figure 2) where the species do not occur. This region is of very recent formation, originating after the Last Glacial Maximum, and consisting of recent sand deposits with constant aeolian dune movement (Seeliger, 1992), which may constrain the dispersion and establishment of many herbaceous plant species, including *E. fulgens*. Herbarium data and personal field excursions did not reveal the presence of the species in the eastern margin of Patos Lagoon. However, as the region is of difficult access, we cannot exclude the possibility of small and scattered populations of *E. fulgens* in the area.

Regarding the east–west range, our data show that *Epidendrum fulgens* is restricted to the coast across most of its geographical range and cannot assume a continental distribution when the inland habitat is formed by forests (i.e. the core BAF, see Figure 1). Nevertheless, the species distribution extends inland within the Pampas grasslands, growing in rock outcrop habitats under relatively dry micro-climatic conditions (Figure 1), a pattern consistent with previous evidence showing the high influence of neighbour formations in the species composition of coastal restingas (Rizzini, 1979; Scarano, 2002). Such extended distribution of *E. fulgens* within the Pampas suggests a specialization for open habitats (shared with species of the subgenus *Amphylottium*, Pinheiro & Cozzolino, 2013) and forest cover as a key factor limiting the species distribution at lower latitudes. Furthermore, we cannot rule out the potential role of biotic interactions in shaping the distribution in the southwest because the small islands of suitable areas predicted by the climatic niche model disappear when accounting for the pollinator richness in the models (see Figure 2).

Our niche model also shows increasing suitability for *E. fulgens* when pollinator richness data are included in the analysis (Figure 2), with a concomitant increase in the overall performance of the analysis when compared to the model using only bioclimatic variables. In fact, pollinator richness shows a peak of diversity at the low-latitude range of *E. fulgens* (Figure 2). The two most informative bioclimatic variables were related to rainfall, which may arrive at 4000mm during the rainy season at the low-latitude distribution range of *E. fulgens* (Joly et al., 2012). Different authors have shown positive effects between rainfall and butterfly abundance in the Neotropics (Brown, 1972; Lourenço et al., 2020). In this scenario, high precipitation levels positively affect the persistence of both *E. fulgens* and its pollinators at the low-latitude range limit. Several butterfly species act as pollinators of *E. fulgens*, which is pollinator-dependent to set fruits. Pollinators also play an important role in cross-pollination, as low levels of inbreeding are observed in this orchid species (Pinheiro

et al., 2011; Sujii et al., 2019). Thus, both bioclimatic variables and pollinator richness apparently do not constrain *E. fulgens* distribution as observed in studies with other species (Lee-Yaw et al., 2017; Sánchez-Castro et al., 2022). However, despite the persistence of populations at this margin, a decrease in the genetic diversity of populations and an increase in genetic differentiation were detected, suggesting constraints in pollen and seed dispersal among populations. Such constraints may increase the adverse effects of drift on genetic diversity, especially at range margins (Bridle & Vines, 2007; Eckert et al., 2008). Furthermore, the low-latitude geographic range limit of *E. fulgens* may have a genetic and/or demographic nature that still requires further investigation.

4.3 | Demographic and genetic limitations of species distribution

Populations in the low-latitude range of *E. fulgens*, mainly Bertioga and Ubatuba (Figure 1), are smaller and patchily distributed compared to central and high-latitude populations (Sujii et al., 2019). According to Willi and Van Buskirk (2019), two main mechanisms may explain the small population sizes at range edges: a decrease in habitat suitability and the geographic pattern of demographic history. As the decrease in the habitat suitability does not limit the species range at this margin (Figures 2 and 4), the historical range contraction and expansion dynamics of tropical forests may have played a role in limiting the habitat of *E. fulgens* in its low-latitude range. Sand dune vegetation at the low-latitude range of *E. fulgens* is currently constrained by the advance of the BAF after the Last Glacial Maximum (Behling, 2002). This pattern gradually changes towards the high-latitude margin, where sand dune vegetation becomes wider (1–10km) and more connected (Seeliger, 1992). Thus, the combination of small, more fragmented populations and restricted habitats in low-latitude populations would decrease the species' resilience to habitat disturbance, such as storms and dune movement (Crawford, 2008). In fact, bottlenecks were detected in low-latitude *E. fulgens* populations (Pinheiro et al., 2011), coupled with the signs of population decline, revealed by a combination of low genetic diversity and non-significant fine-scale genetic structure (FSGS; Sujii et al., 2019). Historical demographic oscillation may negatively impact the level of genetic diversity observed in current populations (Hewitt, 1996) and may predict more accurately the decline in genetic variation towards range distribution edges (Pinheiro et al., 2015).

The low-latitude geographic range of *E. fulgens* also coincides with the high-latitude range limit of a closely related food deceptive species, *Epidendrum denticulatum*, also pollinated by several butterfly species (Pinheiro et al., 2013). Both species hybridize in the contact zone, producing low-viable and sterile hybrids (Pinheiro et al., 2015). In such circumstances, hybridization may translate into severe reproductive costs due to gamete waste (Cozzolino et al., 2022; Sobel et al., 2010). When hybrids are less fit than parentals, natural selection may favour phenotype

combinations that decrease interspecific mating, displacing characters involved in reproduction and reducing the gamete waste, a process called reproductive character displacement (Armbruster & Muchhala, 2008) between well-separated species that have already completed the speciation process, or reinforcement, between incipient closely related species (Hopkins, 2013). However, character displacement and reinforcement may be prevented at range margins due to the stronger effects of drift on small populations, precluding the action of selection (Bridle & Vines, 2007). Thus, in the absence of selection, the adverse effects of gamete waste will persist, with a particularly stronger effect on plant species with generalized pollination (Norton et al., 2015), such as food deceptive species. According to Goldberg and Lande (2006), even low levels of interspecific mating may lead to a sharp parapatric margin due to low levels of reproduction in migrants occurring into the other species' range. Hence, the species cannot establish beyond its geographic range until mechanisms to avoid hybridization have evolved, such as reinforcement or reproductive character displacement (Case & Taper, 2000). The potential negative effects of the biotic interaction between *E. fulgens* and *E. denticulatum* at the low-latitude range limit were not tested here and should be, thus, investigated in future studies.

4.4 | Genetic variation along the species range

We found a significant decrease in genetic diversity (here measured by allelic richness and expected heterozygosity) and an increase in genetic differentiation from the climatic niche and geographical range centres towards the low-latitude limit (Figure 5). Such tendency was also detected towards the high-latitude limit, although with no significance likely due to the lower number of sampled populations (Figure 5). Sujii et al. (2019) also found high levels of FSGS for marginal populations of *E. fulgens*, compared to central ones, which agrees with our results. Genetic diversity and structure indeed vary according to what is expected by the CPH (Pfeilsticker et al., 2021; Pironon et al., 2017; Sujii et al., 2019), likely due to the concordance between geographical peripherality and ecological marginality in *E. fulgens* (i.e. environmental conditions become more different from the centre towards the limits of the species range, Figure 3a). While the low-latitude range may suffer from demographic and genetic constraints caused by historical climate fluctuations and hybridization, the high-latitude range may be severely limited by extreme climate conditions (see discussion above). Although our data have not indicated increased inbreeding rates at the range margins, such a decrease in genetic diversity levels might be limiting the species' evolutionary and adaptive potential—particularly at the rainy edge—which might then limit its expansion further from the current geographical distribution (Blows & Hoffmann, 2005; Gaston, 2009). The abrupt variation of bioclimatic variables at range margins (Figure 3) may also increase the adaptive costs to overcome such environmental differences due to the lack of genetic variation in fragmented peripheral populations caused by drift (Polechová & Barton, 2015).

Another common cause and potentially limiting factor is asymmetric gene flow, considering that dispersal is random and that more gametes should be coming to peripheral and sparse populations than vice versa (Bridle & Vines, 2007; Kirkpatrick & Barton, 1997).

5 | CONCLUSIONS

Our results support the CPH, instigating the debate on distinct factors limiting geographical distribution at the opposite margins of latitudinally distributed species. Bioclimatic variables show contrasting roles between low- and high-latitude range edges, as well as biotic interactions. We found that at the high-latitude limit, the species range is shaped by climate, while at the low-latitude limit, both climate and mutualistic interactions may influence species persistence but cannot explain the range limit. Other positive (i.e. mycorrhiza) or negative (herbivory) biotic interactions and historical factors, although not characterized in this study, may also help explain the distribution limits of *E. fulgens*, particularly at the low-latitude margin. We also found that genetic patterns are in agreement with the predictions of the CPH, with exception of inbreeding rates, which showed no significant declines towards both margins. An improved understanding of how ecological and evolutionary forces limit species distribution ranges along latitudinal gradients is imperative for predicting how species respond to environmental change, especially in fragile tropical ecosystems, such as the resting-gas within the BAF.

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CONFLICT OF INTEREST STATEMENT


No, there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The dataset for this study is available at the following online location (Dryad repository): <https://doi.org/10.5061/dryad.vt4b8gtxg>.

ORCID

Bruno Garcia Luize  <https://orcid.org/0000-0002-8384-8386>

Bárbara Simões Santos Leal  <https://orcid.org/0000-0003-4401-3252>

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BIOSKETCH

This study is part of Jacqueline Salvi de Mattos's doctoral research on the evolutionary biology of the neotropical orchid *Epidendrum fulgens*. This work was carried out at the University of Campinas, Brazil. The authors of this paper share interests in the ecology, evolution and diversification patterns of several plant groups, especially pertaining to the Brazilian Atlantic Forest.

Author contributions: Fabio Pinheiro, Bárbara Simões Santos Leal and Jacqueline Salvi de Mattos conceived the ideas; Jacqueline Salvi de Mattos, Bárbara Simões Santos Leal and Cleber Juliano Neves Chaves collected the data; Jacqueline Salvi de Mattos, Bárbara Simões Santos Leal, Bruno Garcia Luize, Cleber Juliano Neves Chaves, Thales Moreira de Lima and Clarisse Palma da Silva analysed the data; Jacqueline Salvi de Mattos, Bárbara Simões Santos Leal and Fabio Pinheiro led the writing; and Bruno Garcia Luize, Cleber Juliano Neves Chaves, Thales Moreira de Lima and Clarisse Palma da Silva improved the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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