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Geographic and environmental contributions to genomic divergence in mangrove forests

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ABSTRACT

Assessing the relative importance of geographic and environmental factors to the spatial distribution of genetic variation can provide relevant information about the underlying processes that cause and maintain genetic variation in natural populations. With a globally wide but very restricted habitat distribution, mangrove trees are an interesting model for studies aiming to understand the contributions of these factors. Mangroves occur in a narrow range on the continent-ocean interface of tropical and subtropical latitudes, regions considered inhospitable to many other plant types. We employed landscape genomics approaches to investigate the relative contributions of geographic and environmental variables to the genetic structures of two mangrove species, *Avicennia schaueriana* and *A. germinans*, along the Brazilian coast. Using neutral and putative non-neutral single nucleotide polymorphisms (SNPs), we observed significant correlations between the genetic structure and geographical distance, air and sea surface temperatures, solar radiation and tidal variation for both species. In addition, we found that the South Equatorial Current (SEC) acts as a barrier to gene flow among *A. schaueriana* populations. These results increase our knowledge about the evolution of mangrove trees and

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suggest that geographical and environmental variables may shape adaptations of New World *Avicennia* species.

KEYWORDS

Black mangrove; landscape genomics; ocean currents; isolation by environment; gene flow; coastal ecosystem

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INTRODUCTION

Environmental and geographic variations are often determinants of the distribution of allele frequencies in natural populations, facilitating or limiting gene flow across space and influencing the selection of certain genotypes (Murray et al., 2019; Sork, 2016; Wang, Glor, & Losos, 2013). For example, under an Isolation By Distance (IBD) model (Wright, 1943), geographic distance may limit the dispersion and reproductive material of organisms, leading to the accumulation of allele frequency divergences by genetic drift (Bradburd, Ralph, & Coop, 2013). Furthermore, under the Isolation By Barrier (IBB) model, a barrier to gene flow may abruptly reduce or even disrupt connectivity between individuals of a species (Barton, 1979). In addition to these models, landscape components may exert divergent selective pressures on individuals, leading to the evolution of locally adapted populations (Bradburd et al., 2013), a phenomenon described by the Isolation By Environment (IBE) model (Wang & Bradburd, 2014).

These standards, IBD, IBB, and IBE, are not usually mutually exclusive and often co-occur in nature (Sexton, Hangartner, & Hoffmann, 2014; Wang et al., 2013). Determining the contribution of each model to the distribution patterns of genetic variation across space can provide relevant information about the underlying processes that cause and maintain genetic variation in natural populations (Lee & Mitchell-Olds, 2011; Wang & Bradburd, 2014). This knowledge is also essential to predict future responses of current populations to environmental changes (Vincent, Dionne, Kent, Lien, & Bernatchez, 2013) and to minimize biodiversity loss (Kovach, Gharrett, & Tallmon, 2012; Muñoz, Farrell, Heath, & Neff, 2015; Wee et al., 2019).

The field of research that seeks to disentangle the roles of these factors in the distribution of the neutral and adaptive genetic variability of a species over space is known as landscape genomics (Joost et al., 2007; Schoville et al., 2012; Vincent et al., 2013). Recently, this approach

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has been increasingly applied to the study of non-model organisms (Storfer, Patton, & Fraik, 2018). Nevertheless, most landscape genomic studies are limited to animal species, with few such studies on tropical plant species (Storfer, Murphy, Spear, Holderegger, & Waits, 2010) and coastal species such as mangroves, in which adaptive convergences act to allow survival in an environment considered hostile to several other types of plants (Tomlinson, 1986).

Mangrove trees occur in a narrow strip on the continent-ocean interface (Tomlinson, 1986). Mangrove species have the ability to disperse over long distances by river and ocean surface currents (van der Stocken, Wee, et al., 2019) and are found in tropical and subtropical latitudes of the world, mainly between 30 ºN and 30 °S (Giri et al., 2011). The distribution of mangroves is limited by the topography of the intertidal zone (Middleton, 2012), the occurrence of low temperatures (Morrisey et al., 2010) and precipitation patterns (Spalding, Blasco, & Field, 1997). Moreover, there are variations in the latitudes of their boundaries mainly associated with different climatic thresholds (Cavanaugh et al., 2018; Osland et al., 2017) and oceanographic conditions (Soares, Estrada, Fernandez, & Tognella, 2012).

In Brazil, mangroves are distributed along most of the Atlantic coast, from Amapá state (04º 20' N) to Santa Catarina (28º 30' S). Along this latitudinal gradient, six species of mangrove trees belonging to three genera have been found. Among these genera, *Avicennia* L. (Acanthaceae) is one of the most diverse and widely distributed genus globally (Duke, 1991; Li et al., 2016) and is represented on the coast of Brazil by two of the three New World *Avicennia* species, *Avicennia germinans* and *Avicennia schaueriana* (Duke, 1991; Schaeffer-Novelli et al., 1990). These species occur in sympatry on the northeast coast of Brazil. While *A. germinans* has a distribution limit of northern Rio de Janeiro state, *A. schaueriana* extends to the southern state of Santa Catarina.

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Both species show a striking north-south pattern of genetic divergence among populations along the Brazilian coast, as suggested by microsatellite markers (Mori, Zucchi, & Souza, 2015). Similar results were obtained for another mangrove species, *Rhizophora mangle* (Francisco, Mori, Alves, Tambarussi, & de Souza, 2018; Pil et al., 2011), and for the mangrove-associated tree *Hibiscus pernambucensis* (Takayama, Tateishi, Murata, & Kajita, 2008) using the same type of molecular marker. These studies suggested that the neutral genetic divergence may have been convergently shaped by the dispersion of floating propagules in water. When the South Equatorial current (SEC) reaches the Atlantic coast of South America, it splits in two different directions (northwards and southwards) along the coast (Lumpkin & Johnson, 2013). The split of the SEC is concordant with the remarkable genetic divergence observed among the northern and southern populations of mangrove trees along the Brazilian coast.

Using data obtained by next-generation sequencing (NGS), recent studies have identified variable genomic regions possibly associated with adaptive processes relevant in the environmental context of mangroves (Cruz, Mori, Müller, et al., 2019, Cruz, Mori, Oh, et al., 2019). These variations have been attributed to climatic and oceanographic factors that vary widely along the latitudinal gradient of the species distribution.

Although these studies provide clues as to which abiotic factors act to differentiate between *A. schaueriana* and *A. germinans* populations, the contribution of each abiotic factor is still unknown. In this context, the present study aimed to investigate the relative contribution of geographic and environmental variables in the organization of genetic diversity of the two species in the genus *Avicennia* L. (Acanthaceae) found on the Atlantic coast of South America.

MATERIALS AND METHODS

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Biological material and genotyping of SNP markers

The collection of biological material and the identification of single nucleotide polymorphism (SNP) markers were performed in the context of a previous study by Cruz, Mori, Müller, et al. (2019) and Cruz, Mori, Oh, et al. (2019). They sampled 77 *A. schaueriana* individuals from ten different locations and 48 individuals of *A. germinans* from six different locations along the Brazilian coast (Fig. 1 and Table 1). With a minimum coverage of 8x and a minor allele frequency ≥ 0.05, totals of 6170 and 2297 SNP markers were identified for *A. schaueriana* and *A. germinans*, respectively.

Detection of SNP loci with selective signatures

SNP loci with evidence of natural selection were detected by Cruz, Mori, Müller, et al. (2019) and Cruz, Mori, Oh, et al. (2019). For *A. schaueriana*, 86 loci showed considerable deviations from neutral expectations of interpopulation divergence. They were detected by two methods to minimize false positives: LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008), with a confidence interval of 0.99 and a false-discovery rate (FDR) of 0.1, and pcadapt (Luu, Bazin, & Blum, 2017), with a FDR of 0.1. For *A. germinans*, 25 loci showed considerable deviations from neutral expectations of interpopulation divergence. For this species, in addition to LOSITAN (confidence interval of 0.99 and FDR of 0.05) and pcadapt (FDR of 0.05), SNP loci associated with ecological variables were detected using latent factor mixed models (LFMM) implemented in the LEA package (Frichot & François, 2015).

Estimation of genetic distances

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To analyze the importance of geographic distance and environmental variables in spatial genetic divergence, we evaluated which of the models - isolation by distance (IBD), isolation by barrier (IBB) or isolation by environment (IBE) - best describes the genetic diversity of each species based on the SNP markers. For this, we estimated the genetic differentiation (Wright's FST) between pairs of sampling sites (Wright, 1949) for the total set of SNP molecular markers and the set of SNP markers with evidence of selection, using the *Hierfstat* package for R (Goudet, 2005).

Estimation of geographic distances

Pairwise geographic distances between populations were measured using the geographic coordinates of the sampling sites (Table 1) with the global positioning system (Garmin 76CSx, WGS-84 standard, Garmin International Inc., Olathe, KS, USA). Distances between points were estimated based on the contour of the Brazilian coast; thus, dispersion by floating propagules (Duke, Ball, & Ellison, 1998), which are often transported by surface ocean currents (van der Stocken, Carroll, Menemenlis, Simard, & Koedam, 2019), was considered. To determine whether the bifurcation from the southern branch of the SEC to the Brazil current (BC) and the North Brazil current (NBC) (Lumpkin & Johnson, 2013) (Fig. 1) acts as a dispersion barrier for *A. germinans* and *A. schaueriana* propagules, a binary matrix (0 or 1) was constructed based on the presence (1) or absence (0) of the barrier between each pair of sampling sites.

Estimation of environmental distances

To evaluate the effect of the environment, we obtained a total of 37 environmental variables for each sampling site, with a resolution of 30 arc-seconds (~ 1 km in Ecuador). In our

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dataset, we included 28 climate variables derived from the WorldClim temperature and precipitation datasets (version 1.4 and 2.0) (Fick & Hijmans, 2017), 10 oceanographic variables derived the Marspec ocean surface salinity and temperature datasets (Sbrocco & Barber, 2013) and five variables related to tidal variations retrieved from the Environmental Climate Data Sweden (ECDS) platform (Klein et al., 2013). To avoid nonindependence between environmental variables, we removed variables that showed a high correlation ($R^2 > 0.8$), as measured by the *removeCollinearity* function of the *virtualspecies* package (Leroy, Meynard, Bellard, & Courchamp, 2016) for R Core Team (2019). We extracted the values of the environmental variables for our sample points using the *raster* package (Hijmans & van Etten, 2012) for R Core Team (2019). All occurrence data have been carefully inspected to detect and correct problems associated with inconsistent records (Chapman, 2005). We transformed this environmental data matrix using a principal component analysis (PCA) to calculate the Euclidean distances between population pairs (Lira-Noriega & Manthey, 2014). For this calculation, we used the averages of the first five principal components for *A. schaueriana* and the first three principal components for *A. germinans*. Principal component analysis and environmental distance measurements were all performed in R (R Core Team, 2019).

Associative tests

To test which model best explained our genetic data (both neutral and putatively non-neutral), we performed Multiple Matrix Regression with Randomization (MMRR). This method was employed to estimate the independent effect of each factor (geographic or environmental variable) and has been shown to be robust toward a wide range of dispersal rates (Wang, 2013). The analysis was performed using the *MMRR* function in R with 10,000 permutations. The

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following comparisons were made: (I) geographic distance between populations (km) and population differentiation (FST), (II) environmental distance between populations (PCA) and population differentiation (FST), (III) geographic distance (km) and environmental distance (PCA), (IV) geographic distance (km) in conjunction with environmental distance (PCA) and population differentiation (FST) and (V) the presence / absence of the oceanic barrier and population differentiation (FST). We also tested for correlations between the genetic distances based on the SNP marker set with selection evidence for each environmental variable separately.

RESULTS

Genetic, geographic and environmental distances

For the total set of SNP markers, we found FST values between 0.019 and 0.189 for pairs of *A. schaueriana* populations and between 0.047 and 0.387 for pairs of *A. germinans* populations (Fig. 2). For the set of markers with evidence of selection, these values ranged from 0.02 to 0.36 for *A. schaueriana* and from 0.03 to 0.88 for *A. germinans*. The pairwise geographic distances had a maximum value of approximately 5000 km between Bragança - PA (PAR) and Laguna - SC (LGN) for *A. schaueriana* and 2100 km between Ilha de Marajó in Soure – PA (MRJ) and Tamandaré - PE (TMD) for *A. germinans*.

After removing the environmental variables with high correlation ($R^2 > 0.8$), 21 variables were retained for further analyses (Fig. 3). The first five and three axes of PCA based on noncollinear environmental variable matrices explained 96% and 92% of the variance for *A. schaueriana* and *A. germinans*, respectively. The first PCA axis used for the environmental distance calculation among sampling locations of *A. schaueriana* represented 59% of the

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variance (Fig. 4A) and was mainly explained by the water vapor pressure, annual average sea surface temperature, isothermality, average and minimum solar radiation and average annual temperature (Fig. 5A). The second PCA axis represented 15% of the variance (Fig. 4B) and was mainly explained by the average annual tidal cycle duration, annual precipitation and wind speed. For *A. germinans*, the first PCA axis represented 43% of the variance (Fig. 4B) and was mainly explained by the average solar radiation, water vapor pressure, precipitation of the hottest and coldest quarters and wind speed (Fig. 5B). The second PCA axis represented 32% of the variance (Fig. 4B) and was mainly explained by the annual temperature variation, annual average temperature and precipitation seasonality.

Association tests

For *A. schaueriana*, linear regressions between geographic, environmental, and genetic variables for the total set of SNPs revealed a strong correlation between geographic and environmental distances ($R^2 = 0.82$; $P < 0.001$) (Fig. 6A). The geographic distances between pairs of sampling sites played the greatest role in the describing genetic distances (R^2: 0.81, $P < 0.001$) (Fig. 6B), but environmental distance also contributed significantly to genetic distance ($R^2 = 0.56$, $P < 0.001$) (Fig. 6C). When the tests were performed separately for sampling locations above and below the SEC, we found significant correlations only for sampling locations below the SEC between genetic and geographic distances ($R^2 = 0.81$; $P < 0.001$) and between genetic and environmental distances ($R^2 = 0.40$; $P = 0.05$). In relation to genetic distance, multiple regression combining the effects of geographic and environmental distances provided a significantly better fit ($R^2 = 0.84$; $P = 0.0007$) than multiple regressing including only one effect.

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The variable that best explained the genetic differentiation observed in *A. schaueriana* was the presence or absence of the oceanographic barrier ($R^2 = 0.92$, $P = 0.005$).

For *A. germinans*, the correlation between geographic and environmental distances was significant ($R^2 = 0.63$; $P < 0.001$) (Fig. 6D) but was less pronounced than the correlation for *A. schaueriana*, probably due to the smaller number of sampling locations for the former specie than the latter specie. Geographic ($R^2 = 0.61$; $P < 0.05$) (Fig. 6E) and environmental ($R^2 = 0.42$; $P < 0.05$) (Fig. 6F) distances played significant roles in the genetic differentiation between *A. germinans* sampling sites. However, when we removed the samples from Tamandaré - PE, which is located below the SEC, the genetic divergence was not correlated with either the geographic distance ($R^2 = 0.006$; $P = 0.97$) or the environmental distance ($R^2 = 0.014$; $P = 0.70$). Multiple regressions combining the geographic and environmental distances showed a significant correlation ($R^2 = 0.63$; $P = 0.05$) with genetic differentiation, but this correlation was smaller than the correlations observed separately for geographic and genetic divergences. The presence or absence of the oceanic barrier did not explain the genetic divergence among *A. germinans* sampling locations ($R^2 = 0.91$; $P = 0.15$), probably because only one location below the SEC was sampled.

We identified a significant environmental contribution to the genetic differentiation based on the presumably non-neutral SNPs for both species. This contribution was more pronounced for *A. schaueriana* ($R^2 = 0.55$; $P < 0.001$) than for *A. germinans* ($R^2 = 0.38$; $P = 0.05$ 0.15). When we analyzed each environmental variable separately, we found significant correlations of non-neutral genetic differentiation among *A. schaueriana* sampling locations with tidal amplitude cycles, air and ocean surface temperature variations, water vapor pressure, solar

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radiation, and precipitation regimes. The non-neutral genetic differentiation observed in *A. germinans* was significantly correlated with solar radiation and temperature variables (Table 2).

DISCUSSION

The study of the geographic and environmental factors shaping neutral and adaptive genetic variation in heterogeneous environments is one of the main approaches used to understand the dynamics and evolutionary potential of natural populations (Li et al., 2017; Schoville et al., 2012). In this study, we separated the relative contributions of the environment, geographic distance and the presence of an oceanic barrier on the genetic differentiation of populations of two non-model mangrove tree species. We found the relative importance of the main environmental variables that generate adaptation in these species, which is a particularly relevant finding, considering the challenges presented by the climate change predicted for this century.

According to Wright (1978), our pairwise FST results revealed an intermediate degree of genetic differentiation for both species based on the total set of SNP markers, while *A. schaueriana* and *A. germinans* had an intermediate degree and an intermediate to high degree of genetic differentiation, respectively, based on the set of non-neutral SNPs. These results corroborate the genetic structure patterns found in previous studies conducted with neutral molecular markers (Francisco et al., 2018; Mori et al., 2015; Pil et al., 2011; Takayama et al., 2008) and indicate that, regardless of the characteristics of these markers with high (microsatellite) (Vieira, Santini, Diniz, & Munhoz, 2016) or low (SNPs) (Morin, Luikart, Wayne, & The SNP Workshop Group, 2004) mutation rates, the evolutionary processes that led to this divergence must be quite intense or old.

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The geographic distances between sampling sites contributed significantly to the genetic divergence of *A. schaueriana* (R^2: 0.81, $P < 0.001$) and *A. germinans* ($R^2 = 0.61$; $P < 0.05$), suggesting that the isolation by distance (IBD) model (Wright, 1943) plays a fundamental role in the evolution of spatial divergence of these species. This model appears to be typical of mangroves (Cerón-Souza et al., 2010; Kennedy et al., 2016; Ochoa-Zavala, Jaramillo-Correa, Piñero, Nettel-Hernanz, & Núñez-Farfán, 2019; Sandoval-Castro et al., 2014). Although there is evidence of long-distance dispersal by river and ocean surface currents for mangrove species (Mori et al., 2015; Nettel & Dodd, 2007; Takayama, Tamura, Tateishi, Webb, & Kajita, 2013; van der Stocken, Wee, et al., 2019), our results indicate that the large extension of the Brazilian coast limits the dispersal of *Avicennia* species. Although these correlations were significant for the total set of sampling locations, they were not significant when considering only the set of *A. schaueriana* and *A. germinans* sampling locations above the SEC. For the five sampling locations of *A. germinans* in this region, which are distributed in a fairly geographically continuous habitat, little of the model was explained by the coefficient of determination values ($R^2 = 0.006$, $p = 0.97$). We hypothesized that the genetic differentiation between 0.047 and 0.387 observed for all sampling locations could actually be the result of an isolation by barrier (IBB) effect caused by the SEC acting as a barrier to the dispersal of propagules. However, we did not find a significant correlation between genetic differentiation and the presence of the SEC, probably because we sampled *A. germinans* in only one location (Tamandaré - PE) south of the SEC.

In contrast, we found statistical evidence for the action of the SEC as a barrier to gene flow for *A. schaueriana*. Our results corroborate Mori et al. (2015), who suggested that the neutral genetic divergence observed for *A. schaueriana* may have been shaped by marine

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currents. Our results also suggest that the SEC may have a key role in shaping the distribution of genetic variation observed in other species of mangrove or associated with this ecosystem, such as *Rhizophora mangle* (Francisco et al., 2018; Pil et al., 2011) and *Hibiscus pernambucensis* (Takayama et al., 2008). Our findings suggest that the SEC is an important driver of the genetic structure of mangrove species; however, coastal and ocean currents vary temporally in strength and directionality (van der Stocken, Carroll, et al., 2019). For example, The SEC splits, forming the BC and the NBC, which have different speeds and directions (Lumpkin & Johnson, 2013) (Fig. 1). NBC is faster than BC, favoring the spread of propagules from south to north, as observed in previous studies (Francisco et al., 2018; Mori et al., 2015). Therefore, future investigations about the dynamics of these currents, not as a static barrier but including different levels of resistance to gene flow, may provide more accurate information about their influence on the distribution of genetic variation of species dispersed by sea currents.

We also identified an isolation by environment (IBE) pattern in the structure of the genetic diversity of *A. schaueriana* and *A. germinans* that was driven mainly by temperature, radiation and tidal variations along the Brazilian coast. Under the IBE pattern, genetic differentiation increases in response to environmental differences, regardless of geographic distance, and can be generated by a variety of ecological processes, such as selection against immigrants, which implies local adaptation to heterogeneous environments (Wang & Bradburd, 2014). Many species under IBE show local adaptations to environmental gradients (Barker, Frydenberg, Sarup, & Loeschcke, 2011; Byars, Parsons, & Hoffmann, 2009; Jiang et al., 2019; Manthey & Moyle, 2015; Mitchell-Olds, Willis, & Goldstein, 2007; Sexton et al., 2014; Shafer & Wolf, 2013).

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Given the significant results for IBE, we also estimated the contribution of each environmental variable, allowing us to infer the degree to which individual environmental variables contribute to these results. For *A. schaueriana*, we found that genetic variation with evidence of selection is correlated with spatial variations in the tidal range regimes, air and ocean surface temperature, water vapor pressure, solar radiation, and precipitation (Table 2). Our results corroborate Cruz, Mori, Oh, et al. (2019), who analyzed two *A. schaueriana* populations in contrasting regions of the Brazilian coast and found evidence of selection in genes associated with biological processes related to climate seasonality and the response to UV radiation. Conversely, for *A. germinans*, we found correlations between the non-neutral genetic differentiation with variations in solar radiation and temperature patterns (Table 2). The results that we observed for both species corroborate other studies that found precipitation and air and sea temperature variables were limiting factors in the distribution of coastal species (Cavanaugh et al., 2018; Duke et al., 2017; McKee, Rogers, & Saintilan, 2012; Osland et al., 2016; Soares et al., 2012; Ximenes, Ponsoni, Lira, Koedam, & Dahdouh-Guebas, 2018). In addition, our results may serve as a starting point for understanding the adaptations of *Avicennia* species of the South American coast, contributing to the understanding of the evolution of genetic divergence within this genus. Furthermore, this study may guide further investigations about the responses of these species to climate change, such as the predicted increases in the annual average temperatures of air and oceans and the rise in sea level (IPCC, 2014).

CONCLUSIONS

Our results provide strong evidence that IBD and IBE contributed to the evolution of spatial genetic divergence within two *Avicennia* neotropical species on the Atlantic coast of

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South America. A great proportion of the genetic divergence observed within both species may be attributed to IBD. The patterns of genetic divergence were also correlated with variations in the atmospheric temperature, solar radiation and tidal range for both species. In addition, we observed significant correlations with the latitudinal gradient of precipitation and sea surface temperature for *A. schaueriana*, suggesting that IBE also influences the genetic structure of both species. The SEC bifurcation of the Brazilian coast acts as a barrier to gene flow among *A. schaueriana* populations, but we suggest that the SEC speed and direction may be important factors that shape the genetic structure of populations, which requires further investigation. Overall, we provide insights into the relative contributions of environmental and geographic variables that influence the processes maintaining the distribution of genetic diversity within *A. schaueriana* and *A. germinans* in the Atlantic coast of South America.

DATA ARCHIVING STATEMENT

Data strings supporting these findings can be found in GenBank with the primary access codes GSE116060 and GSE123659 for *A. schaueriana* and *A. germinans*, respectively.

ACKNOWLEDGMENTS

We thank Alessandro Alves Pereira and Prianda Laborda for critically reading the manuscript. This study was financed in part by the Coordination for the Improvement of Higher Education Personnel - CAPES Computational Biology Program (88887.177151 / 2018-00) and by São Paulo Research Foundation - FAPESP (2018 / 18431-1).

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TABLES

Table 1. Collection sites for the samples of *Avicennia germinans* and *A. schaueriana* long the Brazilian Atlantic coast.

Avicennia schaueriana	**Locality (City/State)**	**Latitude**	**Longitude**	**Location in Fig. 1**
PAR	Bragança, Pará	-0.82	-46.61555556	1s
ALC	Alcântara, Maranhão	-2.410277778	-44.40611111	2s
PRC	Paracuru, Ceará	-3.413055556	-39.05638889	3s
VER	Vera Cruz, Bahia	-12.98361111	-38.68472222	4s
GPM	Guapimirim, Rio de Janeiro	-22.70138889	-43.00722222	5s
UBA	Ubatuba, São Paulo	-23.48944444	-45.16444444	6s
CNN	Cananéia, São Paulo	-25.02	-47.91805556	7s
PPR	Pontal do Paraná, Paraná	-25.575	-48.3525	8s
FLN	Florianópolis, Santa Catarina	-27.57694444	-48.51888889	9s
LGN	Laguna, Santa Catarina	-28.4451	-48.84008667	10s
Avicennia germinans	**Locality (City/State)**	**Latitude**	**Longitude**	**Location in Fig. 1**
MRJ	Soure, Pará	-0.7238889	-48.49	1g
PAb	Bragança, Pará	-0.9047222	-46.6875	2g
ALC	Alcântara, Maranhão	-2.4102778	-44.40611	3g
PNB	Parnaíba, Piauí	-2.778333	-41.822222	4g
PRC	Paracuru, Ceará	-3.4130556	-39.05639	5g
TMD	Tamandaré, Pernambuco	-8.5263889	-35.01333	6g

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Table 2. Linear regressions between each environmental variable and genetic distances based on the set of molecular markers with evidence of natural selection in *Avicennia schaueriana* and *A. germinans*.

Environmental variables	*A. schaueriana*		*A. germinans*	
	R^2	p - value	R^2	p - value
Annual mean temperature (C°)	0.45	**0.0009**	0.81	**0.01**
Temperature annual range (C°)	0.36	**0.0004**	0.04	0.63
Isothermality (C°)	0.75	**0.0005**	0.50	0.09
Mean diurnal range (C°)	0.006	0.74	0.24	0.27
Max temperature of warmest month (C°)	0.003	0.63	0.80	**0.03**
Annual precipitation (mm)	0.012	0.54	0.09	0.33
Precipitation seasonality (mm)	0.56	**0.0004**	0.24	0.28
Precipitation of warmest quarter (mm)	0.31	**0.008**	0.91	0.06
Precipitation of coldest quarter (mm)	0.39	**0.01**	0.008	0.88
Mean solar radiation (kJ m^{-2} day^{-1})	0.44	**0.0005**	0.63	**0.03**
Min solar radiation (kJ m^{-2} day^{-1})	0.49	**0.0001**	0.03	0.58
Max solar radiation (kJ m^{-2} day^{-1})	0.23	**0.006**	0.86	**0.05**
Wind speed (m s^{-1})	0.037	0.42	0.07	0.41
Water vapor pressure mean (kPa)	0.53	**0.0005**	0.085	0.45
Mean annual SSS (psu)	0.00008	0.96	0.002	0.68
SSS of the saltiest month (psu)	0.015	0.48	0.096	0.23
Annual variance in SSS (psu)	0.036	0.5	0.096	0.22
Mean annual SST (C°)	0.46	**0.001**	0.007	0.81
SST of the warmest month (C°)	0.27	**0.005**	0.014	0.93

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Annual average cycle amplitude (cm)	0.62	**0.0007**	0.12	**0.0006**
Annual average duration of tidal cycles (h)	0.1	0.12	0.035	0.74

Significant values are presented in bold. *SST = sea surface temperature. *SSS = sea surface salinity

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FIGURE LEGENDS

Fig. 1. Map showing the geographical distribution of *Avicennia schaueriana* (pink) and its sympatric region with *A. germinans* (pink and yellow) on the South Atlantic coast and the geographic locations of collection sites for the *A. schaueriana* (green circles) and *A. germinans* (red circles) plant material used for genetic analyses ((Cruz, Mori, Müller, et al., 2019; Cruz, Mori, Oh, et al., 2019). Sampling locations are displayed according to Table 1. Arrows represent the direction of the main ocean currents acting on the Brazilian coast. Arrow widths illustrate the mean current speed (Lumpkin & Johnson, 2013).

Fig. 2. Interpopulation genetic differentiation based on the total set of molecular markers estimated by a pairwise FST (Wright) for (A) *A. schaueriana* and (B) *A. germinans* collection sites.

Fig. 3. Dendrograms showing the groups (red boxes) of correlated ($R^2 > 0.8$) environmental variables retrieved from public data platforms: (A) WorldClim version 1.4, (B) WorldClim version 2.0 (Fick & Hijmans, 2017), (C) Marspec (Sbrocco & Barber, 2013), and (D) ECDS (Klein et al., 2013).

Fig. 4. Principal component analysis based on Euclidean distances estimated from a matrix of 21 environmental variables for sampling sites of (A) *A. schaueriana* and (B) *A. germinans*. The acronyms for sampling locations are the same as those in Table 1.

Fig. 5. Contribution of noncollinear environmental variables to the first principal component of the PCA for (A) *A. schaueriana* and (B) *A. germinans*. *SST = Sea surface temperature. *SSS = Sea surface salinity.

Fig. 6. Linear regressions (blue lines) and standard deviation (gray shadow) of pairwise comparisons of sampling locations (A) between geographic and environmental distances, (B)

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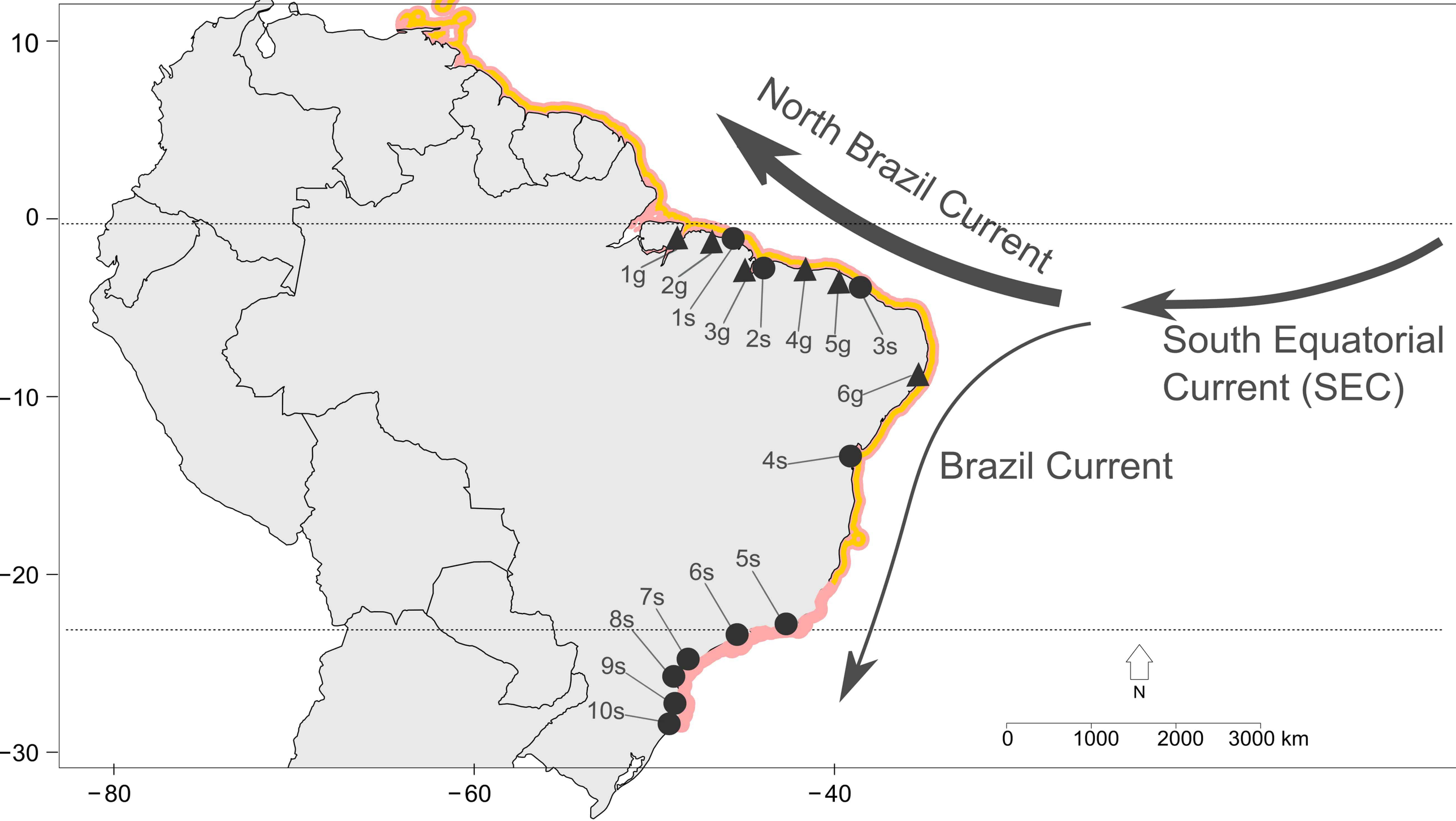
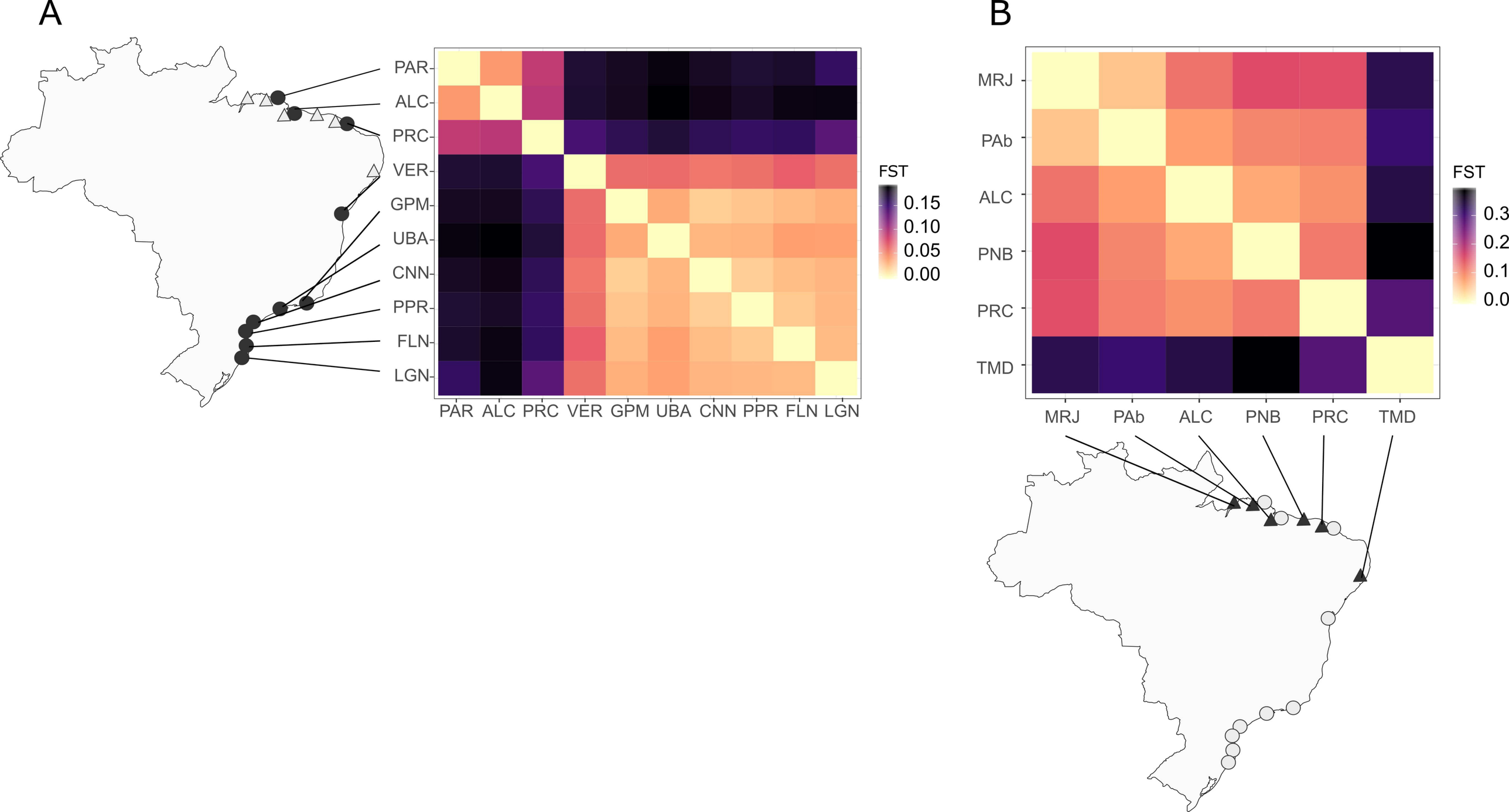
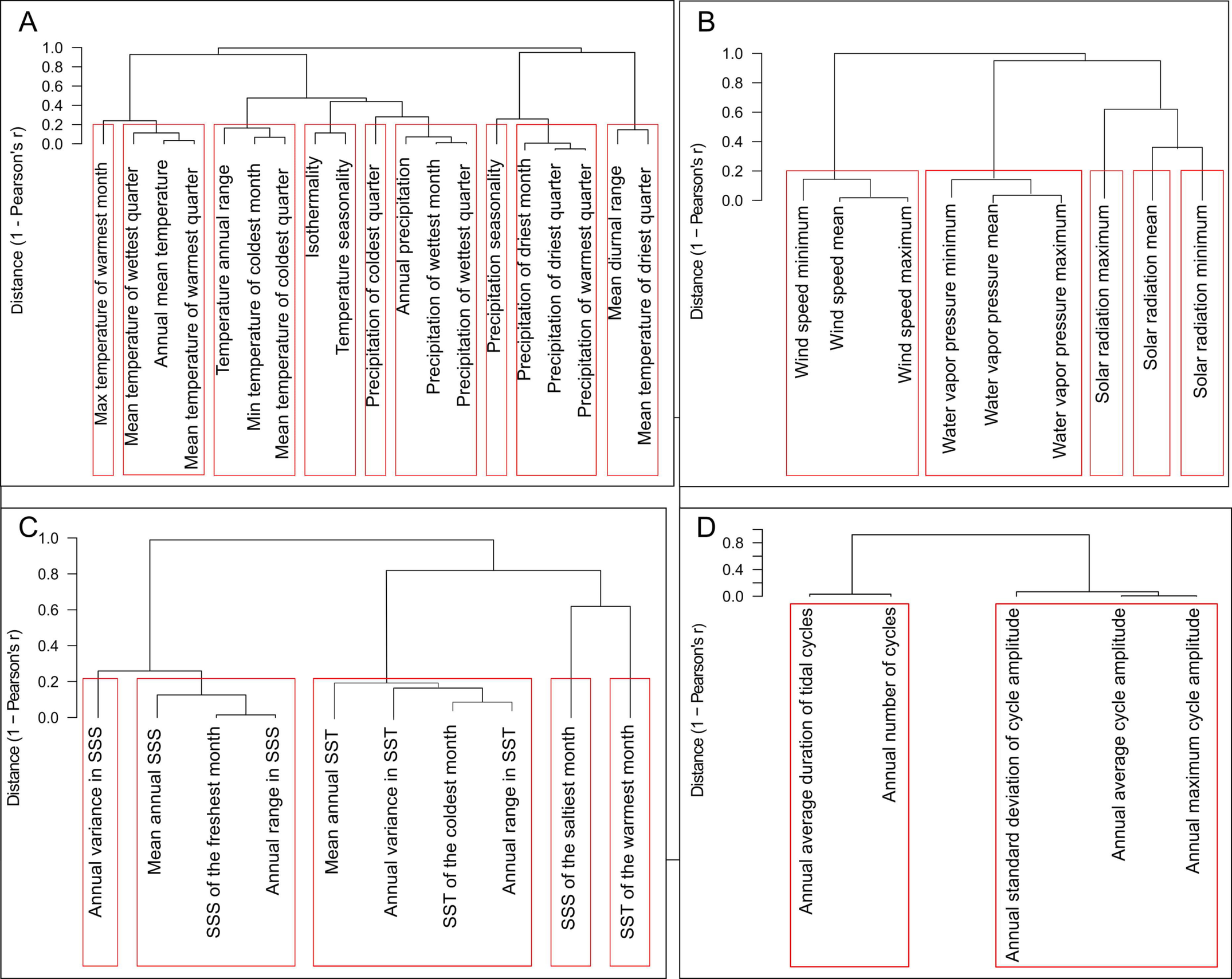
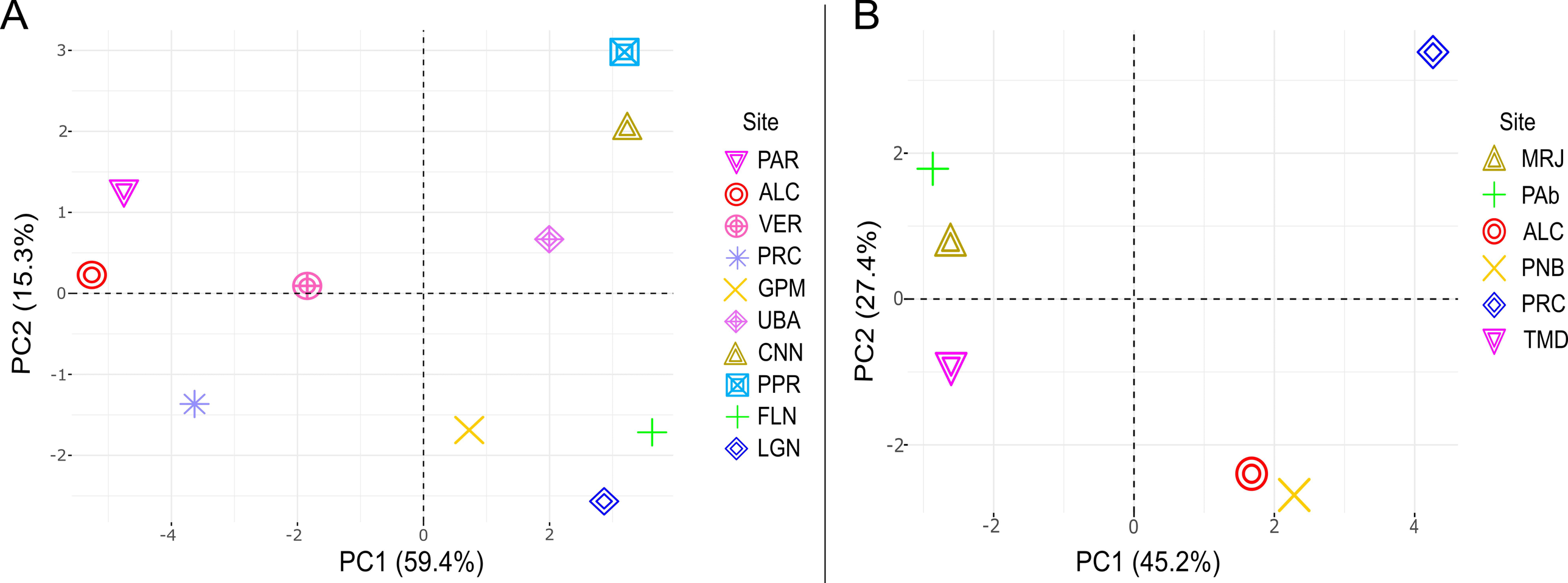
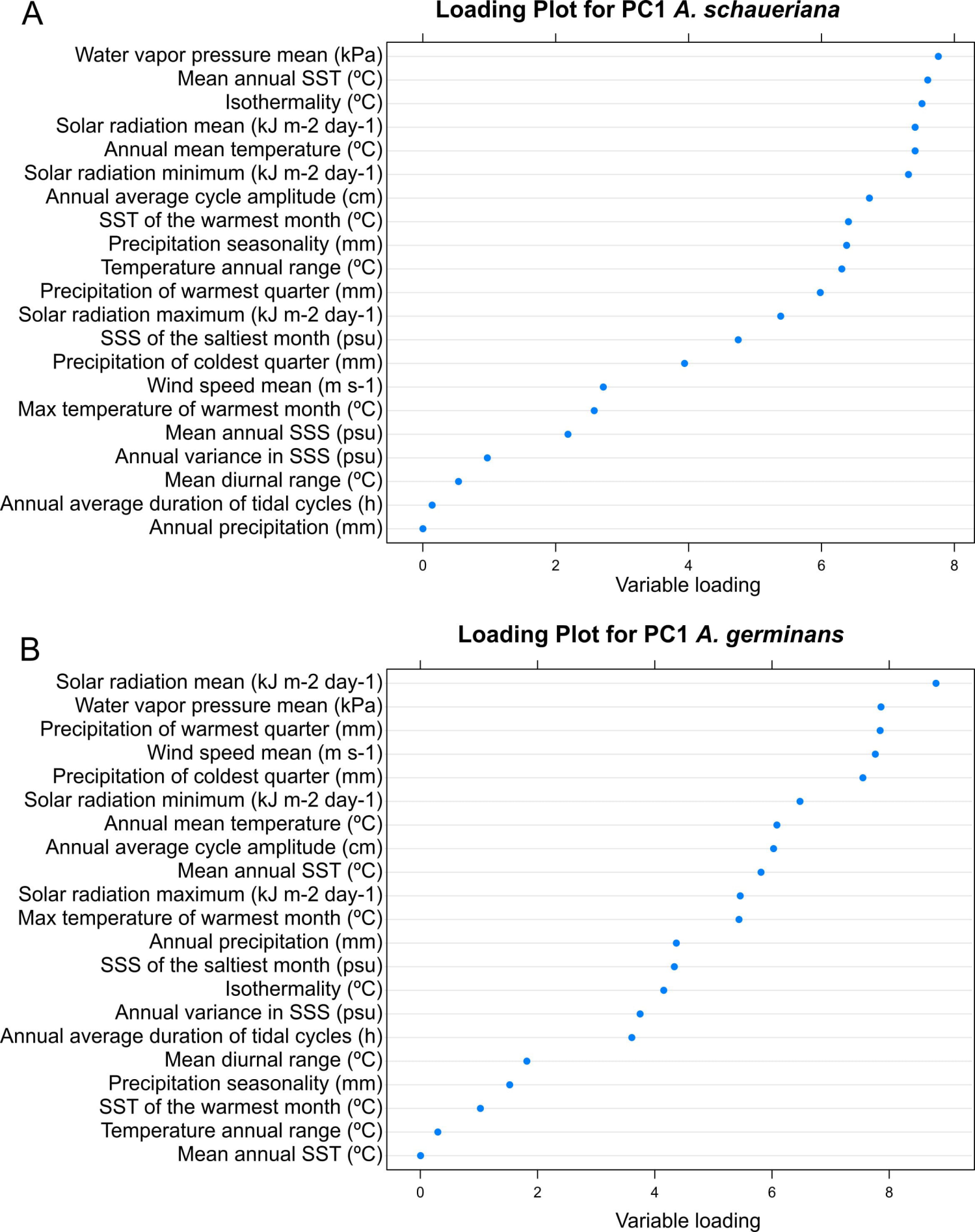
between geographic and genetic distances and (C) between environmental and genetic distances for *A. schaueriana* and (D) between geographic and environmental distances, (E) between geographic and genetic distances and (F) between environmental and genetic distances for *A. germinans.*

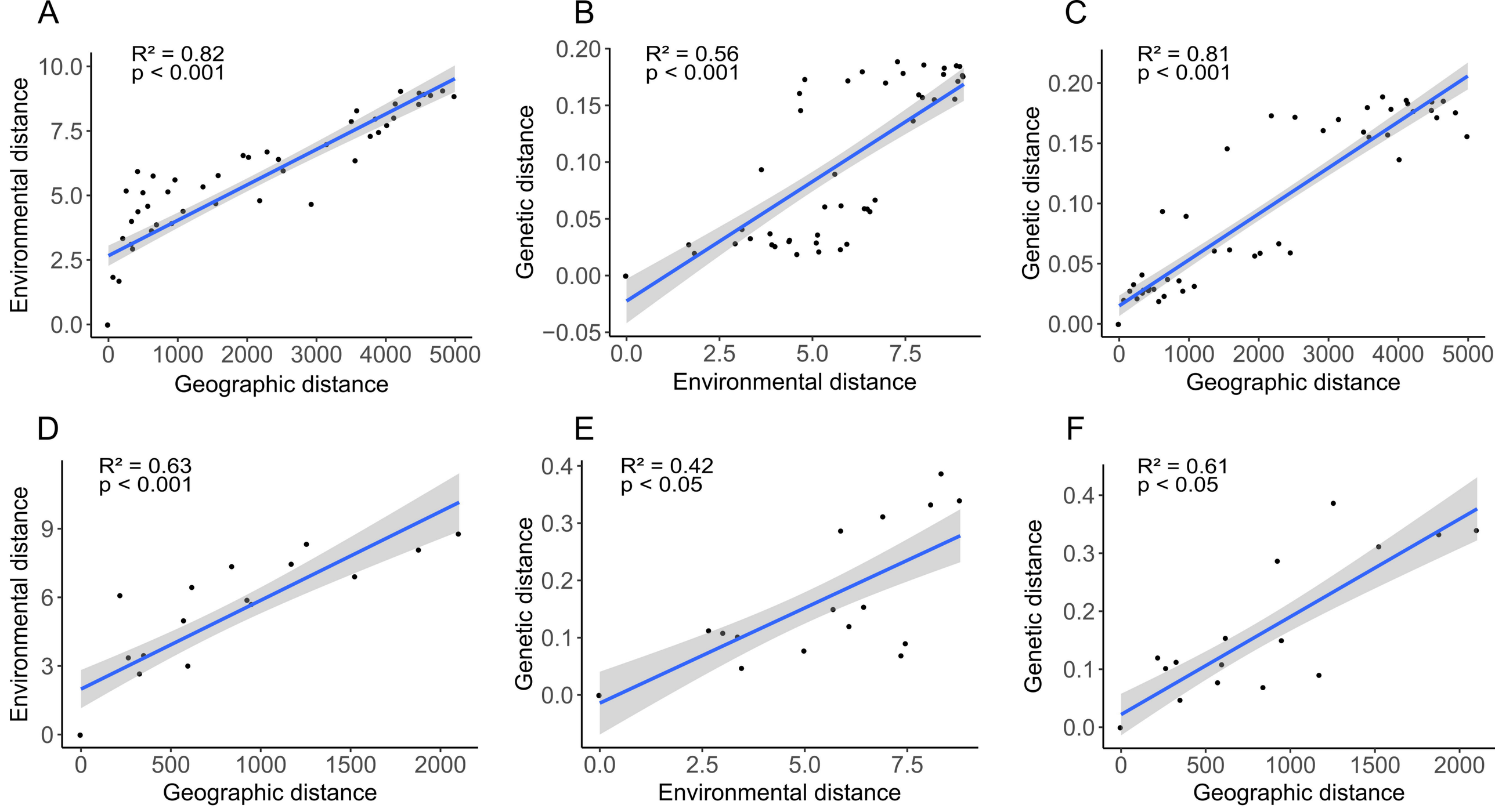

North Brazil Current
South Equatorial Current (SEC)
Brazil Current
1g
2g
1s
3g
2s
4g
5g
3s
6g
4s
5s
6s
7s
8s
9s
10s
N
0
1000
2000
3000 km
10
0
−10
−20
−30
−80
−60
−40


A
PAR
ALC
PRC
VER
GPM
UBA
CNN
PPR
FLN
LGN
FST
0.15
0.10
0.05
0.00
B
MRJ
PAb
ALC
PNB
PRC
TMD
FST


A
Distance (1 - Pearson's r)
1.0
0.8
0.6
0.4
0.2
0.0
Max temperature of warmest month
Mean temperature of wettest quarter
Annual mean temperature
Mean temperature of warmest quarter
Temperature annual range
Min temperature of coldest month
Mean temperature of coldest quarter
Isothermality
Temperature seasonality
Precipitation of coldest quarter
Annual precipitation
Precipitation of wettest month
Precipitation of wettest quarter
Precipitation seasonality
Precipitation of driest month
Precipitation of driest quarter
Precipitation of warmest quarter
Mean diurnal range
Mean temperature of driest quarter
B
Distance (1 – Pearson's r)
1.0
0.8
0.6
0.4
0.2
0.0
Wind speed minimum
Wind speed mean
Wind speed maximum
Water vapor pressure minimum
Water vapor pressure mean
Water vapor pressure maximum
Solar radiation maximum
Solar radiation mean
Solar radiation minimum
C
Distance (1 – Pearson's r)
1.0
0.8
0.6
0.4
0.2
0.0
Annual variance in SSS
Mean annual SSS
SSS of the freshest month
Annual range in SSS
Mean annual SST
Annual variance in SST
SST of the coldest month
Annual range in SST
SSS of the saltiest month
SST of the warmest month
D
Distance (1 – Pearson's r)
0.8
0.4
0.0
Annual average duration of tidal cycles
Annual number of cycles
Annual standard deviation of cycle amplitude
Annual average cycle amplitude
Annual maximum cycle amplitude


A
PC2 (15.3%)
PC1 (59.4%)
3
2
1
0
-1
-2
-4
-2
0
2
Site
PAR
ALC
VER
PRC
GPM
UBA
CNN
PPR
FLN
LGN
B
PC2 (27.4%)
PC1 (45.2%)
2
0
-2
-2
0
2
4
Site
MRJ
PAb
ALC
PNB
PRC
TMD


A
Loading Plot for PC1 A. schaueriana
Water vapor pressure mean (kPa)
Mean annual SST (ºC)
Isothermality (ºC)
Solar radiation mean (kJ m-2 day-1)
Annual mean temperature (ºC)
Solar radiation minimum (kJ m-2 day-1)
Annual average cycle amplitude (cm)
SST of the warmest month (ºC)
Precipitation seasonality (mm)
Temperature annual range (ºC)
Precipitation of warmest quarter (mm)
Solar radiation maximum (kJ m-2 day-1)
SSS of the saltiest month (psu)
Precipitation of coldest quarter (mm)
Wind speed mean (m s-1)
Max temperature of warmest month (ºC)
Mean annual SSS (psu)
Annual variance in SSS (psu)
Mean diurnal range (ºC)
Annual average duration of tidal cycles (h)
Annual precipitation (mm)
0
2
4
6
8
Variable loading
B
Loading Plot for PC1 A. germinans
Solar radiation mean (kJ m-2 day-1)
Water vapor pressure mean (kPa)
Precipitation of warmest quarter (mm)
Wind speed mean (m s-1)
Precipitation of coldest quarter (mm)
Solar radiation minimum (kJ m-2 day-1)
Annual mean temperature (ºC)
Annual average cycle amplitude (cm)
Mean annual SST (ºC)
Solar radiation maximum (kJ m-2 day-1)
Max temperature of warmest month (ºC)
Annual precipitation (mm)
SSS of the saltiest month (psu)
Isothermality (ºC)
Annual variance in SSS (psu)
Annual average duration of tidal cycles (h)
Mean diurnal range (ºC)
Precipitation seasonality (mm)
SST of the warmest month (ºC)
Temperature annual range (ºC)
Mean annual SST (ºC)
0
2
4
6
8
Variable loading


A
R² = 0.82
p < 0.001
Environmental distance
Geographic distance
B
R² = 0.56
p < 0.001
Genetic distance
Environmental distance
C
R² = 0.81
p < 0.001
Genetic distance
Geographic distance
D
R² = 0.63
p < 0.001
Environmental distance
Geographic distance
E
R² = 0.42
p < 0.05
Genetic distance
Environmental distance
F
R² = 0.61
p < 0.05
Genetic distance
Geographic distance