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To cite this article: Jéssica Fernanda Ramos Coelho , Sergio Maia Queiroz Lima & Flávia de Figueiredo Petean (2020): Phylogenetic conservatism of abiotic niche in sympatric Southwestern Atlantic skates, Marine Biology Research, DOI: [10.1080/17451000.2020.1837883](https://doi.org/10.1080/17451000.2020.1837883)

To link to this article: <https://doi.org/10.1080/17451000.2020.1837883>



Published online: 26 Nov 2020.



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ORIGINAL ARTICLE



Phylogenetic conservatism of abiotic niche in sympatric Southwestern Atlantic skates

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ABSTRACT

From the perspective of phylogenetic niche conservatism (PNC), closely related species must share more aspects of a niche than randomly expected. However, considering the competitive exclusion principle, PNC is questionable for related species in sympatry. This research aimed to test PNC in Riorajini, a tribe of four skates endemic to the Southwestern Atlantic Ocean: *Atlantoraja castelnaui*, *A. cyclophora*, *A. platana*, and *Rioraja agassizii*. We updated available distribution maps for these species with literature data, reconstructed the phylogenetic relationships of the group with genetic data (*mt-nd2*), modelled the ecological niche (ENM) of each species, and calculated niche overlap, equivalency and similarity between models. The results recovered Riorajini as a monophyletic group and indicated PNC with bathymetry, distance to shore and concentration of nitrate characterizing the tribe's abiotic niche. However, no linear relationship between phylogenetic proximity and niche similarity was clear since pairs of species more phylogenetically distant showed more similar niches (*R. agassizii* and *A. castelnaui*, > 70% niche similarity, $P < 0.005$) than congeners (*A. castelnaui* and *A. platana*, 45%, $P < 0.005$). ENMs of each species showed different responses to variations in environmental predictors, with *A. castelnaui* and *R. agassizii* showing higher probability of occurrence in shallower waters, closer to shore, while *A. cyclophora* and *A. platana* explore deeper areas, although still constrained to the continental shelf. We discuss how these differences influence the distribution of each species in the environment and used the phylogeny to argue that *R. agassizii* and *A. castelnaui* share a conserved niche from an ancestral lineage.

ARTICLE HISTORY

Received 18 June 2020
Accepted 9 October 2020

KEYWORDS

Coexistence; ecological niche model; Grinnellian niche; Neotropical coastal zone; threatened species

Introduction

Phylogenetic niche conservatism (PNC) is a lineage's likelihood of maintaining ancestral niche features through time (Harvey and Pagel 1991). Numerous studies exploring this idea have been published, typically testing whether closely related species share more aspects of a niche than stochastically expected (e.g. Ahmadzadeh et al. 2013; Peixoto et al. 2017). In a scenario of rapid climate changes this is an important issue to investigate, considering that groups showing PNC track these changes faster, and as such has implications for biodiversity patterns of distribution (Parmesan and Yohe 2003; Chivers et al. 2017). Reviews on the niche conservatism topic indicate that PNC is ubiquitous in nature (Peterson 2011), although the vast majority of studies are focused on terrestrial organisms (Prinzing et al. 2001; Lovette and Hochachka 2006;

Patterson and Givnish 2007; Rödder and Lötters 2009; Khaliq et al. 2015; da Silva et al. 2020), with few recently published exceptions exclusively testing this issue for marine taxa (e.g. Hopkins et al. 2014; Wang et al. 2015; Buser et al. 2019; Lu et al. 2019). To some extent, this hinders our ability to discuss this matter in the aquatic environment, which makes an empirical test of niche conservatism important for marine clades.

Considering that two species cannot coexist if they occupy the same niche, the well-known 'competitive exclusion principle' (Kneitel 2008), it is expected that niche conservatism is unlikely between sympatric sister-species, for which niche divergence is probably the rule for coexistence (Losos et al. 2003; Pigot and Tobias 2013; Scriven et al. 2016). In the marine environment, abiotic conditions rapidly change with increasing depth of seafloor, influencing community

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Supplemental data for this article can be accessed at <https://doi.org/10.1080/17451000.2020.1837883>

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composition and population dynamics along the environmental gradient (Smith and Brown 2002). Environmental heterogeneity has also been recognized to influence populations' genetic diversity, structure and speciation (Rocha et al. 2005; Ortego et al. 2012; Temunović et al. 2012; Pyron et al. 2015), and in species-rich regions this heterogeneity may provide the means for niche partition, decreasing inter-specific competition and facilitating coexistence of competitive species.

The Southwestern Atlantic Ocean (SWA) is one of these regions of high environmental heterogeneity, with a coastal zone marked by the influences of the Brazilian and Malvinas currents, variation in salinity given the high freshwater discharge of the La Plata river, and bathymetric variation to the edge of the continental shelf (Brandini et al. 2000). This region is divided into two provinces – Warm Temperate Southwestern Atlantic and Magellanic – which together encompass nine ecoregions harbouring a highly variable biota (Spalding et al. 2007). Such variability in both environmental characteristics and life forms makes the littoral of the SWA a good system to investigate the differences in ecological niches of species occurring in the same geographic space. The SWA also hosts the highest number of threatened chondrichthyan species in the Neotropical region (Field et al. 2009), and due to its high richness, endemism and number of threatened species, Stein et al. (2018) classified the SWA as a priority area for conservation of cartilaginous fish.

Skates are elasmobranchs of benthic habits occurring in coastal marine regions as well as in the deep-sea (Ebert and Compagno 2007; Last et al. 2016). Besides depth, water temperature and salinity likewise affect elasmobranchs' distribution, and shifts from a species' optimum set of environmental conditions can impact behaviour, physiology and metabolic functioning (Green and Jutfelt 2014; Pistevos et al. 2015). Understanding species' abiotic preferences (also called Grinnellian niche; Grinnell 1917) is important to comprehend their geographic distribution and physiological aspects, as well as to predict their ecological role in an ecosystem (Dumbrell et al. 2010). Such characterizations are also fundamental to understand community interactions, and to estimate the impacts of environmental changes on species (Harmon et al. 2009; Rinnan and Lawler 2019).

The tribe Riorajini *sensu* McEachran and Dunn (1998) includes four skates endemic to the SWA in a monophyletic group within the family Arhynchobatidae (Naylor et al. 2012a): *Rioraja agassizii* (Müller &

Henle, 1841), *Atlantoraja platana* (Günther, 1880), *A. cyclophora* (Regan, 1903) and *A. castelnaui* (Miranda Ribeiro, 1907). Despite differences in mean body size and the natural ontogenetic diet shift, Riorajini species converge in the consumption of the same prey items, mostly crustaceans (amphipods, shrimps, brachyurans), teleosts, and, to a lesser extent, *A. castelnaui* also feeds on cephalopods and other elasmobranchs (Barbini and Lucifora 2011, 2012, 2016; Viana and Vianna 2014; Viana et al. 2017). Changes in diet have been noticed seasonally, although it is more likely to be a consequence of prey availability and behaviour rather than change in preferences by these skates (Barbini and Lucifora 2012). As a consequence of high fishing pressure, all Riorajini species are threatened: *A. cyclophora*, *A. platana* and *R. agassizii* are classified as 'Vulnerable' (Massa et al. 2006; Kyne et al. 2007; San Martín et al. 2007), and the larger *A. castelnaui* as 'Endangered' (Hozbor et al. 2004). This, combined with a limited geographic distribution and life-history traits, such as slow growth, late maturity and limited dispersal ability, makes skates one of the most vulnerable taxa of all marine species (Stevens et al. 2000; Dulvy et al. 2014).

Although biological aspects of the tribe Riorajini are well-documented in the literature (e.g. Oddone and Vooren 2004, 2005; Oddone and Amorim 2007; Oddone and Capapé 2011; Viana and Vianna 2014; Moreira et al. 2017), their geographic distribution presents a shortfall to be addressed. According to International Union for Conservation of Nature (IUCN) maps, these four species are distributed in the SWA roughly from the coast of Espírito Santo State in Brazil to Patagonia in Argentina (Hozbor et al. 2004; Massa et al. 2006; Kyne et al. 2007; San Martín et al. 2007). However, some of these maps are outdated and do not include records from recent literature (e.g. Bovcon et al. 2011), which can underestimate the area of occurrence of these species. Accuracy on range of occurrence is crucial to inform future conservation actions for these threatened species, and such uncertainties about the geographic distribution of species characterize a Wallacean shortfall (Hortal et al. 2015). Other aspects, such as biological characteristics and adaptation to benthic habits, suggest that Riorajini species explore similar resources, thus they are likely to play similar ecological roles in the environment (Rosenfeld 2002). However, sympatry in a limited geographic range raises the question on which aspects of niche allow their co-occurrence.

The scarcity of studies exploring PNC for marine groups highlights the importance of the present

work, and reveals a gap in the literature that demands research efforts. Our research is the first to apply a modelling approach to identify and discuss PNC in Chondrichthyes. As the term ‘niche’ can assume multiple meanings, when testing for conservatism it is important to highlight the concept and also the phylogenetic scale at which it is discussed, because results may vary with taxonomic level and/or temporal scale used, as well as with the dimension of niche that is observed (Wang et al. 2015; Peixoto et al. 2017; Graham et al. 2018). In our study, we consider the Grinnellian niche concept, which focuses on abiotic and climatic conditions necessary for a species to survive (Soberón 2007), and we test PNC at the level of tribe.

We hypothesize that an abiotic niche divergence plays an important role in the sympatry of this group by guiding species to different strata or drivers in the environment (Scriven et al. 2016). To test this, we first need precise information (georeferenced data) on where each of these four species occur and their abiotic niches. Therefore, the aims of the present research are to (i) provide updated geographic distribution maps of these threatened species incorporating data available in the literature, (ii) reconstruct the molecular phylogeny of the group, and characterize their abiotic niche to assess niche conservatism in Riorajini.

Materials and methods

Phylogenetic analysis

We used sequences of *NADH dehydrogenase 2, mitochondrial (mt-nd2)* from Riorajini skates available on GenBank, all from Naylor et al. (2012a) where there is an analysis of genetic distance of an extensive number of Elasmobranchs’ representatives. By Naylor et al. (2012b)’s phylogenetic inference, the existence of four lineages within Riorajini is noticeable. No other molecular marker for the whole tribe was available in GenBank, our primary source of data. Because chondrichthyans have slow rates of evolution (Martin et al. 1992), a longer and faster molecular marker, such as the *mt-nd2* (Broughton and Reneau 2006; Naylor et al. 2012a), can provide more variation in comparison to *cytochrome c oxidase I, mitochondrial (mt-co1)*, commonly used in other organisms (Moore et al. 2011). Therefore, the usage of *mt-nd2* only should bring satisfactory hypotheses on the phylogenetic relationships among these lineages. We chose *Sympterygia acuta* Garman, 1877 as an outgroup for the phylogenetic analysis, a skate of the same family

of the Riorajini tribe (Naylor et al. 2012a), also occurring in sympatry (Massa and Hozbor 2004). Sequences were retrieved under the following accession numbers: *Atlantoraja castelnaui* (JQ519082.1), *A. cyclophora* (JQ519084.1), *A. platana* (JQ519083.1), *Rioraja agassizii* (JQ519080.1) and *S. acuta* (JQ519081.1).

We used MEGA 7.0.26 (Kumar et al. 2016) to align the sequences using the ClustalW method (Larkin et al. 2007). The same software was used to select the molecular evolution model under the Bayesian Inference Criteria (BIC) (Luo et al. 2010), which indicated Hasegawa-Kishino-Yano with Gamma distribution (HKY+G) as the best model. To infer phylogenetic relationships under a Bayesian analysis, we used BEAST version 1.10.4 (Suchard et al. 2018), and ran 10^7 generations sampled every 1,000, with a burn-in of 10%. We used FigTree version 1.4.0 (Rambaut and Drummond 2012) to edit the tree.

Data collection

Occurrence records

Occurrence data for each species derived from online databases, such as Global Biodiversity Information Facility (GBIF 2020), *speciesLink* (CRIA 2020) and FishNet2 (Fishnet2 Portal 2017), and the literature (full set of compiled records in Supplementary Material, Table SI). We conducted an exploratory analysis to remove discrepant values (outliers) using *vegan* package version 2.5.2 in R (Oksanen et al. 2013). Duplicates and redundant points (i.e. points in the same grid cell) were removed to increase data uniformity of distribution and avoid spatial autocorrelation (Shcheglovitova and Anderson 2013). Additionally, we used *spThin* package version 0.1 in R to return the best dataset of occurrence records per species (Aiello-Lammens et al. 2015). These procedures avoid biasing the model towards areas of easier access and higher sampling effort by removing aggregations of one species’ occurrence records.

In an attempt to increase accuracy, data from online databases were only considered for preserved specimens deposited in fish collections or museums, georeferenced in each species’ known occurrence area (Brazil, Uruguay, and Argentina coasts). Remarkable morphological differences between the species of this group, evidenced by well-defined species diagnoses, as well as notably different patterns of dorsal colouration (e.g. Figueiredo 1977; Gomes et al. 2010), aggregates trustworthiness to the identification of the specimens. All data per species were plotted in marine biogeographic provinces as in Spalding et al. (2007).

Environmental data

The environmental layers used are variables, also called predictors, that characterize the abiotic conditions of the region to be modelled. Bio-ORACLE (Tyberghein et al. 2012; Assis et al. 2018) and MARSPEC (Sbrocco and Barber 2013) are online platforms that offer high resolution (5-arc-min and 30-arc-sec, respectively) environmental layers for the present climatic and geophysical marine conditions. Each layer is a raster file derived from satellite data that were scaled to equal dimension and resolution (0.833°, ~9 km), and cropped between 70°W–30°W and 58°S–10°S to reflect the tribe's area of actual and potential occurrence.

There is no consensual guideline regarding the ideal number of predictors for niche models. However, the selection of environmental layers must consider aspects of the species' biology and ecology (Fourcade et al. 2018), and the question to be answered (Merow et al. 2013). Besides, from a model-performance's point-of-view, the selection of predictors must be conducted in a way to avoid model overfitting and multicollinearity, which can happen when the number of predictors is much higher than the number of occurrence points in a dataset (Parolo et al. 2008), or when variables are correlated (Warren et al. 2014), respectively. Thus, a Pearson correlation test was performed with 30 available layers (18 from MARSPEC and 12 from Bio-ORACLE, the latter corresponding to mean, maximum and minimum values of benthic maximum depth variables) for current geo-climatic conditions to remove highly correlated ones ($|r| \geq 0.8$). Even without strong correlation with remaining variables, layers with immediate appearance of no relevance for the clade (e.g. plan curvature) were manually removed. The removal of one from a pair of highly correlated variables considered ecological and biological knowledge of the clade (Oddone and Vooren 2004; Oddone and Amorim 2007). Nine uncorrelated variables were then selected to run the models. We used box plots to visualize and manually remove remaining outlier records of occurrence once the environmental variables were chosen.

Ecological niche models (ENMs)

R program version 3.5.1 (R Core Team 2018) was used as an interface for a machine-learning algorithm to build maximum entropy (maxent) models of ecological niche (ENMs) (Phillips et al. 2006). ENMs were conducted using species' records (presence) and data characterizing the environment it occupies, following a correlative approach (Pearson 2007).

Following Muscarella et al. (2014), we tested six combinations of maxent's feature classes (FC): L, H, LQ, LQH, LQHP, LQHPT (L: linear; H: hinge; Q: quadratic; P: product; T: threshold). Feature classes represent raw or modified values of environmental variables. For each FC combination, we tested eight values of regularization multiplier (varying from 0.5 to 4.0, with a 0.5 increment). Regularization multiplier (RM or β) decreases overfitting of models (Merow et al. 2013). *ENMeval* package was used to choose the best combination of parameters (FC and RM) per model (Muscarella et al. 2014), and the combination to generate the most parsimonious model ($\Delta AICc = 0$) was considered the best. Models' training and testing points were partitioned applying the 'block' method (Muscarella et al. 2014). Models were run with a 10^{-5} convergence threshold, 10,000 maximum iterations, and 10,000 maximum background points. Each model is a mean of 15 bootstrap replicates. Maps were edited with QGIS 2.8.9 software (QGIS Development Team 2019).

Comparing niches – testing niche conservatism

For our purposes, we considered the Grinnellian niche concept. We conducted a principal component analysis (PCA) to reduce dataset dimensions (Jolliffe and Cadima 2016), and visualize the divergence between centroids of distribution of each species and the set of environmental layers selected. The first principal components explaining more than 70% of the proportion of variance (PV) of the data were kept in the analysis (Zuur et al. 2010). Eigenvectors showing $|PV| \geq 0.4$ in at least one principal component were kept. Data heteroscedasticity was confirmed using *bio-tools* package version 3.1 in R (da Silva et al. 2017), thus we used the non-parametric permutational multivariate analysis of variance (PERMANOVA) to identify which centroids were significantly different in the PCA.

Following Boennimann's et al. (2012) framework, we conducted a variation of a principal component analysis (PCA-env) to compare the niches of Riorajini species, which allows to test niche equivalency and niche similarity between species pairs. The test of niche equivalency determines whether the two niches compared are identical based on the species geographic occurrences (Warren et al. 2008). Considering a pair of species, the niche equivalency test compares their true equivalency to a null distribution of niche equivalency scores created from pooling their occurrence records, then randomly resampling those to create two datasets keeping the number of records from the original samples. If the measured value (true equivalency) differs significantly ($P < 0.05$)

from those of the null distribution, we have ecologically distinct species (Wielstra et al. 2012). The niche similarity test, otherwise, measures whether two species occupy niches that are more similar than expected at random considering the background space where they occur (Warren et al. 2008). For this, the true (calculated) similarity is compared with a null distribution of similarity scores created by measuring the overlap between the niche of one species and the background space of the second species. If $P < 0.05$, we have higher similarity than stochastically expected in a phylogeny. Both tests of niche equivalency and similarity are based on 100 repetitions to create the null distributions of simulated values (Broennimann et al. 2012; Wielstra et al. 2012).

The Schoener's D index was calculated to measure the degree of niche overlap between models of species' pairs (Warren et al. 2008), whose values vary from 0 (no overlap) to 1 (identical models). Both Schoener's D index and PCA-env analyses were conducted using *ecospat* package version 3.0 in R (Di Cola et al. 2017). We performed a Mantel test to evaluate a correlation between phylogenetic relationships and niche similarity and equivalency scores (1000 replicates) using *ade4* 1.7.13 and *ape* 5.3 packages in R (Chessel et al. 2004; Paradis and Schliep 2019). We tested the null hypothesis of absence of connection between genetic distance and niche similarity, then between genetic distance and niche equivalency.

Results

Phylogeny

The Bayesian phylogenetic inference recovered the same topology of relationships among Riorajini species (Figure 1) proposed by Naylor et al. (2012b), with *Atlantoraja platana* closely related to *A. cyclophora*, *A. castelnaui* as sister to this clade, and *Rioraja agassizii* as sister-genera to this group. All nodes have high posterior probabilities (> 0.97), the analysis had a good mixing and high ESS (> 1500) for all statistics checked in Tracer 1.7.1 (Rambaut et al. 2018).

Geographic distribution

Coupling data from online biodiversity databases and literature (Table S1), occurrence records for Riorajini species expanded 5° southward for *A. castelnaui*, and $\sim 3^\circ$ north for *A. platana*, both compared with distribution maps currently available (e.g. IUCN and Fish-Base maps) (Figure 2). There is a gap in occurrence data of *A. platana* in the north of the Argentinean coast, across Mar del Plata, which was not evident in these previously published maps of distribution. For *A. cyclophora*, we found registered occurrences slightly south of its IUCN map of distribution, near Bahía Blanca in the Argentinean coast (Barbini and Lucifora 2016). There are no outstanding differences between maps of *R. agassizii*, which presented the most uniform

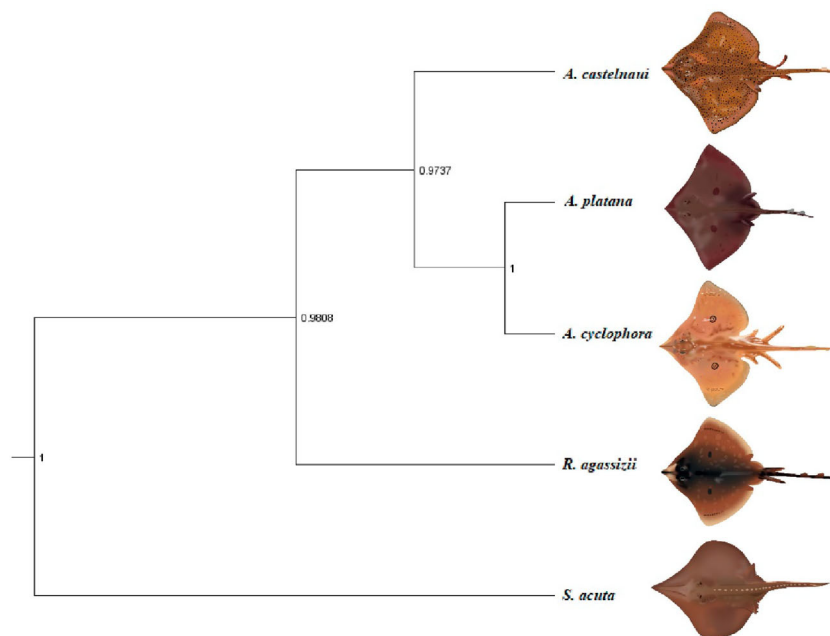


Figure 1. Phylogeny of Riorajini based on a Bayesian inference using the gene *NADH dehydrogenase 2, mitochondrial (mt-nd2)*, including *Sympterygia acuta* as outgroup. Node values as posterior probabilities. Skates drawings by Felipe Coelho.

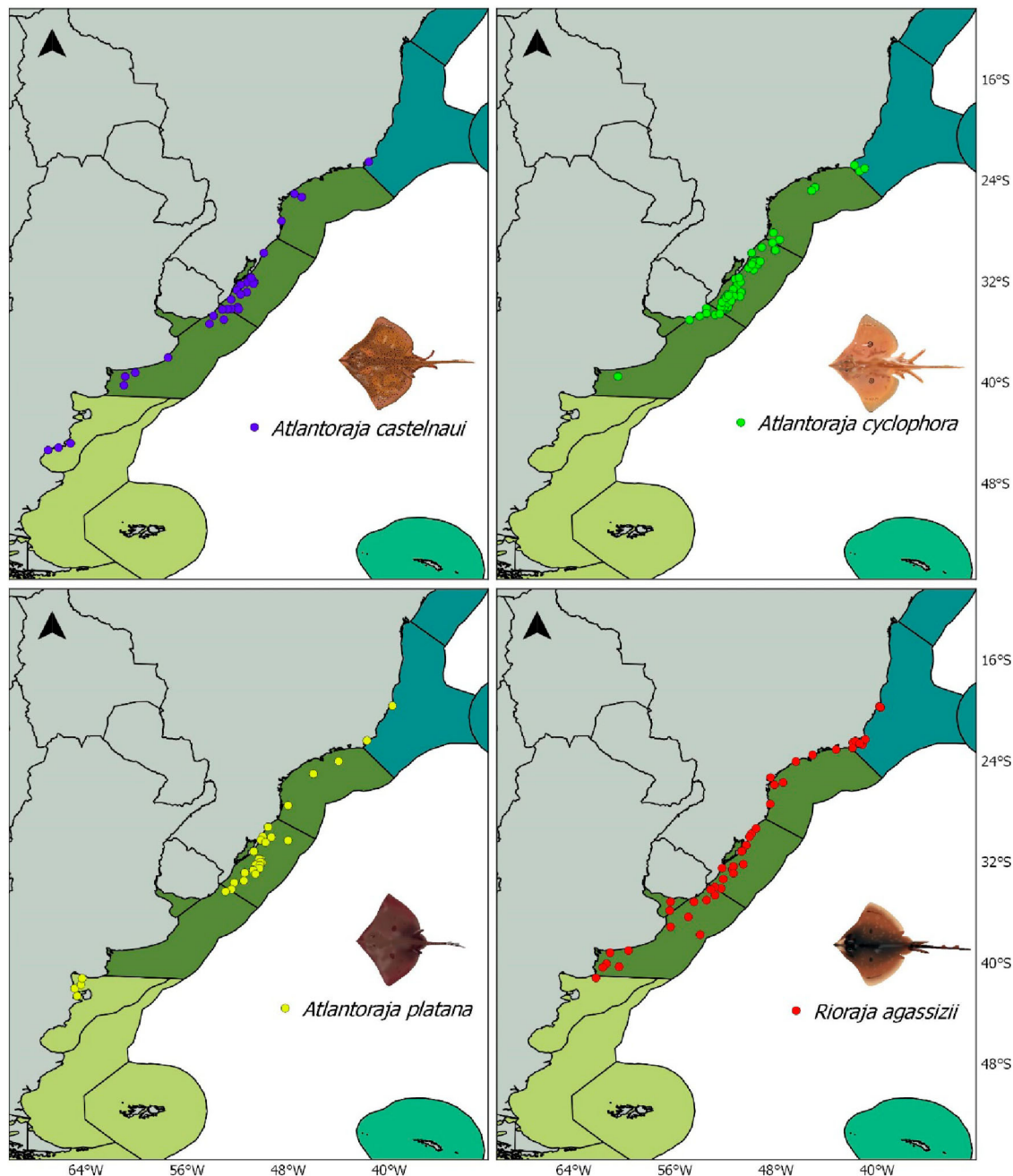


Figure 2. Occurrence records of preserved specimens used for the ecological niche models of *Atlantoraja castelnaui*, *A. cyclophora*, *A. platana* and *Rioraja agassizii* along the marine provinces (Spalding et al. 2007) in the Southwestern Atlantic Ocean.

distribution of occurrence points along its area of occupancy (Figure 2). All four species occur mainly in the Warm Temperate Southwestern Atlantic (WTSA) province, from the south-eastern coast of Brazil to the Uruguay-Buenos Aires shelf, but there are also a few records in the Tropical Southwestern Atlantic and Magellanic provinces, slightly north and south, respectively, of the WTSA province (Spalding et al. 2007) (Figure 2).

Results of the principal component analysis (PCA) (Figure 3) show centroids of distribution significantly

differed ($P < 0.05$) for all pairwise comparisons of species, except for *A. cyclophora* and *A. platana*, for which we could not reject the null hypothesis of centroids' equivalency based on the PERMANOVA results.

Ecological niche models (ENMs)

Nine uncorrelated ($|r| \leq 0.8$) environmental layers were selected for modelling the ecological niche of *Atlantoraja castelnaui*, *A. cyclophora*, *A. platana* and *Rioraja agassizii*. The best model ($\Delta AICc = 0$) of each species

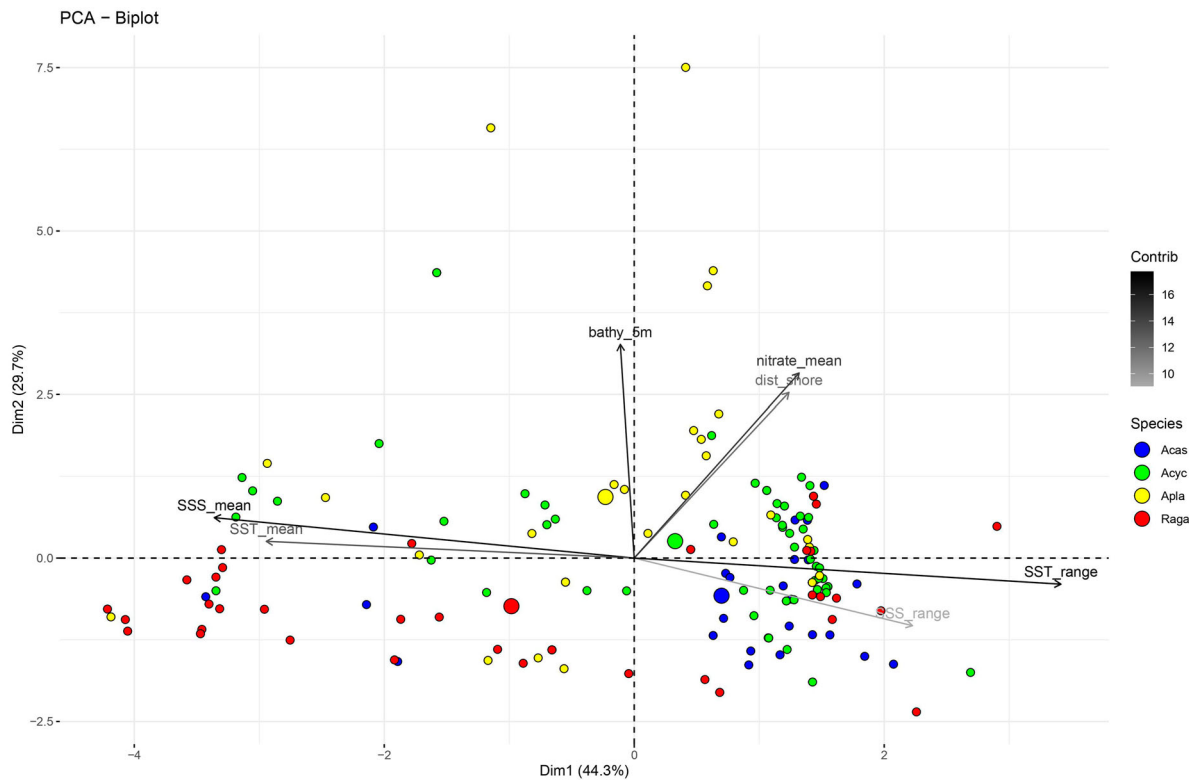


Figure 3. Principal component analysis (PCA) illustrating the influence of environmental variables for *Atlantoraja castelnaui* (Acas), *A. cyclophora* (Acyc), *A. platana* (Apla) and *Rioraja agassizii* (Raga). Largest circles are the centroids of distribution of the scattered points. Centroids position are significantly different from one another except in Acyc–Apla (PERMANOVA, $P > 0.05$). Contrib: contribution of environmental variables (vectors), with darker shades indicating stronger contribution.

presented a different combination of parameters, and the ENM of each species (Figure 4) presented a different set of environmental variables with the highest contribution to the model ($> 70\%$, measured as the permutation importance) (Table I). The SWA region where the tribe Riorajini occurs is under the influence of the freshwater outflow of the La Plata river, between Uruguay and Argentina, which impacts environmental heterogeneity and provides a plethora of niches to explore. This is reflected in species' niches presenting different responses to variations in environmental characteristics.

For the nine variables included in the ENMs, five were the most significant for all species, characterizing the fundamental abiotic niche of the group: nitrate concentration, depth of seafloor (bathymetry), distance to shore, and, to a lesser extent, temperature range and salinity range. As aforementioned, the importance of each of these predictors varied between species and up to three variables were necessary to characterize the niche of each species by more than 70% (Table I), which we consider to be

the abiotic conditions that exert higher influence in the realized abiotic niche of each species.

Niche overlap and similarity results showed that the four species present abiotic niches that highly overlap and are more similar than expected by chance (Figure 5). However, *R. agassizii* differed significantly from *A. castelnaui* and *A. cyclophora* ($P < 0.05$) based on the niche equivalency test (Table SII). In other words, despite high overlap and similarity, the ecological niches of these species are not the same. Besides, there is no indication of correlation between genetic distance and niche similarity nor equivalency by Mantel tests ($R = 0.16$, $P = 0.26$; and $R = -0.35$, $P = 0.67$, respectively).

Overall, our results indicate conservatism of abiotic niche in the tribe Riorajini. However, a linear relationship between phylogenetic closeness and niche similarity is not always clear, since some pairs of species more phylogenetically distant show highly similar niches, whereas congeners display more divergent niches. Abiotic niches varied between species, although such variation occurred within a limited subset of environmental variables.

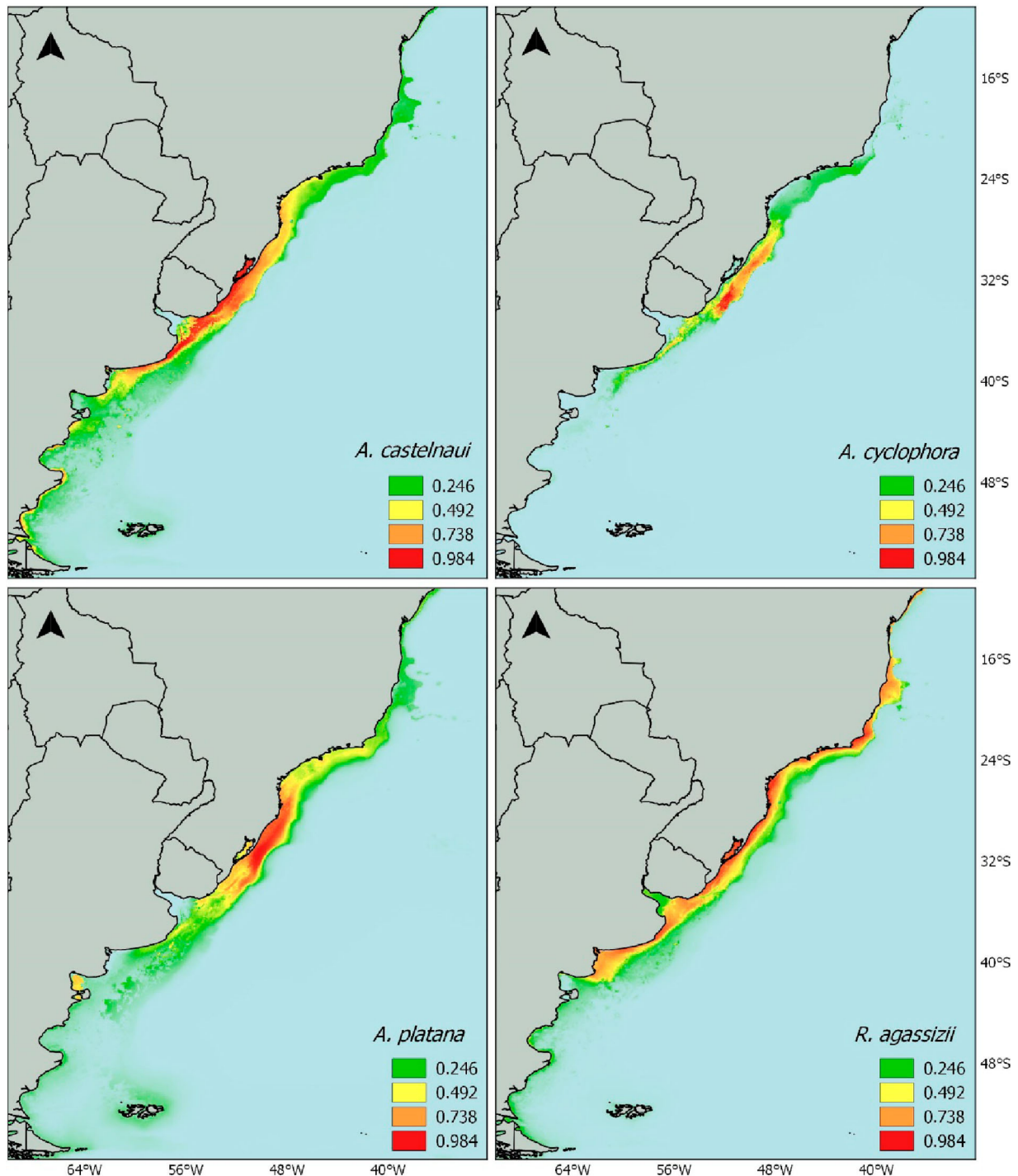


Figure 4. Ecological niche models of *Atlantoraja castelnaui*, *A. cyclophora*, *A. platana* and *Rioraja agassizii* in the Southwestern Atlantic Ocean. Warmer colours indicate higher probability of occurrence of a given species.

Discussion

Phylogenetic niche conservatism (PNC) in Riorajini

In Riorajini, congeners present abiotic niches that are more equivalent and similar than stochastically expected, suggesting this is a dimension of niche

that is phylogenetically conserved between these species (Wiens and Graham 2005). Stronger dissimilarities can be found with regards to equivalency between species of different genera. However, these differences do not outweigh high similarity and overlap, even between these species of different genera. For example, *Atlantoraja castelnaui* and *Rioraja agassizii*

Table 1. Permutation importance (%) of each environmental variable (lines) selected after Pearson's correlation test ($|r| \geq 0.8$) for the ecological niche model per species (last four columns). *Acas*: *Atlantoraja castelnaui*; *Acyc*: *A. cyclophora*; *Apla*: *A. platana*; *Raga*: *Rioraja agassizii*. Bold highlights the variables of higher contribution ($\Sigma > 70\%$) to the models of each species.

	Unit	Scale	Code	Species			
				<i>Acas</i>	<i>Acyc</i>	<i>Apla</i>	<i>Raga</i>
Temperature mean	°C	100×	SST_mean	1.6	4.5	8.9	2.6
Temperature range	°C	100×	SST_range	18.2	3.2	1.7	0.1
Salinity mean	psu	100×	SSS_mean	0.2	0.5	0.4	0.3
Salinity range	psu	100×	SSS_range	0.1	1.4	1.2	11.7
Distance to shore	km	1×	dist_shore	12.2	2	26.5	30.6
Depth of seafloor	m	1×	bathy_5m	19.6	3.8	53.6	33.7
Nitrate mean	mol.m ⁻³	1×	nitrate_mean	37.1	80.1	0.1	20.2
Iron mean	mol.m ⁻³	1×	iron_mean	10.9	3.1	7.5	0.5
Current velocity	m ⁻¹	1×	current_vel	0.1	1.4	0.1	0.2

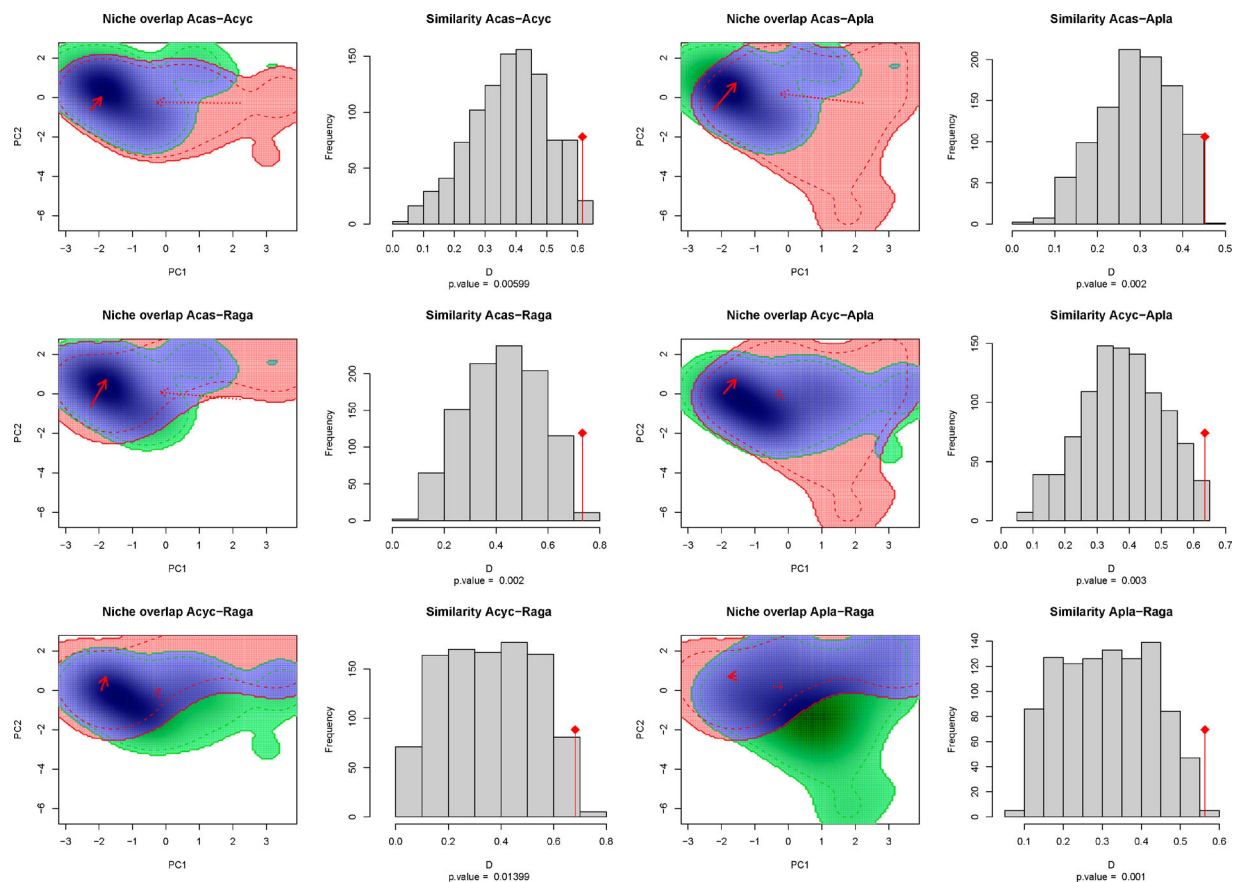


Figure 5. PCA-env results of niche overlap and niche similarity tests for each pair of Riorajini species. The gridded niche of the first species in a pair is in green; the second, in red; overlap between the two niches is in blue. Arrows point to the direction of shift for the centroids of distribution. *Acas*: *Atlantoraja castelnaui*; *Acyc*: *A. cyclophora*; *Apla*: *A. platana*; and *Raga*: *Rioraja agassizii*.

showed the highest similarity (~72%) of niches, despite not being equivalent. Both species occur in shallow waters, close to the shoreline (Colonello et al. 2007; Barbini and Lucifora 2012); however, *A. castelnaui* reaches about 116 cm of total length (TL) (Oddone and Amorim 2007), making it the largest species of this tribe, while *R. agassizii* is the smallest, reaching up to 71 cm TL (Weigmann 2016). Body size has an important effect on skates' ecological

role in the environment (Barbini et al. 2018), thus these biological and habitat characteristics may illustrate the meaning of high similarity without equivalency of niches. A resembling pattern of high similarity without equivalency between niches of phylogenetically close lineages was found by Aguirre-Gutiérrez et al. (2015) study with pines, for which the authors argue non-interchangeability of niches between species in spite of high similarity. In that study,

however, the five pine species analysed are congeners and niche overlaps were, overall, very low for all pairwise comparisons.

Coupling results of niche similarity and equivalency within a phylogenetic perspective, it is more parsimonious to assume that an ancestral lineage had a niche that is conserved by *R. agassizii* and *A. castelnaui*, and the sister-clade to *A. castelnaui* evolved a distinct feature, which is shared by *A. cyclophora* and *A. platana*. These two pairs of species differ in preferable habitats, with *R. agassizii* and *A. castelnaui* occurring in shallower waters in comparison to *A. cyclophora* and *A. platana*, which explore the continental shelf further (Oddone and Vooren 2004; Oddone and Amorim 2007). Differences in depth of occurrence have been mentioned for these species in the literature (Menni et al. 2010) and, as a general pattern for elasmobranchs, Smith and Brown (2002) found a negative relationship between bathymetry and body size – larger species occurring in shallower waters.

Such differences driving pairs of species to separate strata in the environment can exert a relaxation in inter-specific competition for resources, as suggested for other groups of closely related species occurring in sympatry for which niche conservatism is predominant (Lovette and Hochachka 2006). This is relevant considering other dimensions of niche that highly overlap between these species, such as their trophic niche. Species-level differences of abiotic niche seem to compensate the similarities in other aspects of niche that could be detrimental to the exploration of resources for these sympatric competitive species, although we do not argue such differences triggered lineage divergence and diversification in the group, for which other prezygotic barriers (e.g. different clasper structures; Moreira et al. 2017) might have played a role during speciation, and later ecological differentiation evolved (Peterson et al. 1999). To better picture their evolutionary history, further studies with these species should consider including a more comprehensive phylogeny (i.e. incorporating more molecular markers and individuals), considering that Moreira et al. (2017) have cast doubt on the tribe's relationships.

PNC is also evoked to explain patterns of species richness (Buckley et al. 2010) and diversity (Kozak and Wiens 2010; Khaliq et al. 2015; Morinière et al. 2016) because it can constrain an organism's ability to disperse and colonize regions that are different from their places of origin (Wiens and Graham 2005; Crisp et al. 2009; Daru et al. 2017). Skates are the most diverse group within batoids and yet present highly conserved morphological and ecological

characters (Ebert and Compagno 2007; Ball et al. 2016), as we corroborate with our results, in which the abiotic niches are conserved within the group. In Riorajini, a reduction of rostral cartilage and extension of pectoral radials, the former considered a paedomorphism, are conserved morphological characters that suggest adaptation to benthic habitats (McEachran and Dunn 1998). Buser et al. (2019) argue the role of 'constraints on morphological and ecological evolution' to explain the tendency of niche conservatism even between different habitats (marine and freshwater) for cottoid fish. If similar forces are at play for skates, conservatism of abiotic niche is likely to be widespread in the group; however, further studies are needed to elucidate this and, especially, to estimate the extent to which such patterns can be unfavourable to this group's ability to cope with rapid global climate changes (Wiens and Graham 2005).

In this sense, conservatism of abiotic niche does not seem to impair the sympatry of Riorajini; however, it may jeopardize the tribe's ability of thermal adaptability in a global warming scenario, which later can lead to drastic changes in community composition and structure. Some niche features evolve slower than others, and habitat-related traits are among those of higher lability (Blomberg et al. 2003; Ripa 2019). Nevertheless, given previously described biological and ecological characteristics of skates (e.g. Stevens et al. 2000; Dulvy et al. 2014), we can safely assume that the evolution of such adaptive traits are unlikely for the group in the short period of time imposed by climatic changes (Quintero and Wiens 2013), and that these temperate water species would need more generations to efficiently acclimate to new abiotic conditions. Instead, because these species present conserved climatic niches, they track environmental conditions more closely (Chivers et al. 2017) and are, therefore, more likely to respond to global warming pressures by shifting geographic ranges, a pattern observed for other marine taxa (Perry et al. 2005; Nicolas et al. 2011). This indicates Riorajini species are likely to undergo profound changes in geographic distribution in a global warming context, with potential negative impacts to composition and structure of their local community. In an ongoing research we are testing the group's specific response to climate changes (Coelho et al. in prep.).

Environmental drivers of occurrence and distribution

Each Riorajini species showed a different set of environmental variables influencing their probability

of occurrence. However, these differences occurred within a fraction of the environmental niches available, which reflects both the tribe's conserved abiotic niche, and the variety of vacant niches in the environment. Pyron et al. (2015) defined as 'constrained' niches those of closely related species that vary within a subset of a shared fundamental niche. High overlap and similarity between niches of Riorajini species can imply some redundancy in ecological function, which benefits community resilience (Matich et al. 2017). This means that, in the absence of one species, others of similar ecological roles are likely to fill in. On the downside for this tribe, environmental changes may affect these different species similarly as they present overlapping abiotic niches and geographic distribution.

Mean concentration of nitrate was an important aspect to characterize the abiotic niche of Riorajini, for which species presented higher probability of occurrence for low values of this variable (Figure S1). Low concentrations of nitrate in SWA near the shoreline reflect the influence of the Brazilian Current flowing southward along a shallow continental shelf (Brandini et al. 2000). Tropical waters in the Brazilian current are oligotrophic and present low concentrations of suspended particles, which also indicate that the influx of organic matter from land does not affect the water in this current (Seeliger et al. 1998). On the other hand, the Malvinas Current, reaching the south of WTSA province and flowing northward, is rich in dissolved nutrients and, therefore, sustains primary productivity and a vast food chain in the region (Seeliger et al. 1998). As a consequence, high availability of prey in this region might decrease competition caused by dietary overlap between these species.

It is important to highlight the gap in geographic distribution of *A. platana* in the north of the Argentinean coast, across Mar del Plata (Figure 2). Paesch et al. (2014) analysed 25 years of data on the frequency of occurrence of Chondrichthyes along the common fishing area between Uruguay and Argentina and showed *A. platana* occurring only in the Northern Zone of this area (Uruguayan coast), being absent in the River Zone (La Plata river mouth) and Southern Zone (north of Argentinean coast). The other Riorajini species occur in all three zones, although with different frequencies of occurrence in each of them (Paesch et al. 2014).

In fact, the ENM for *A. platana* shows a break in environmental suitability for its occurrence across the La Plata region (Figure 4), with a later increase in probability of occurrence in San Matías Gulf, where Estalles

et al. (2011) found *A. platana* to be the most abundant Riorajini species. These authors also cited a personal observation by Collier stating that this isolated population in San Matías Gulf is the only known occurrence of this species in the Argentinean Sea, which suggests that this distribution gap represents a true absence, although the idea of insufficient sampling effort for the southern coast of Argentina, or misidentification of young specimens cannot be discarded, given high similarity between young of *A. platana* and *R. agassizii* (Oddone MC 2019, pers. comm.). If such a gap represents true absence of this species, the population at Magellanic province might be isolated, which can imply genetic structuring. Such insight illustrates the potential application of ENMs for phylogeographic studies (Alvarado-Serrano and Knowles 2014).

Despite their fundamental importance for understanding ecosystems dynamics and species biology, data registering the occurrence of elasmobranchs are often a by-product of fisheries statistics. Perhaps for this reason the process of mapping the distribution of species is not yet entirely automated, evidenced by outdated maps for some species in renowned, popular websites of biological information (e.g. IUCN and FishBase). Although these websites are of unquestionable importance, a literature review is crucial before referring to them to ensure the maps available are fit for this purpose. For Riorajini, previous maps of distribution mostly failed to illustrate the latitudinal limits of occurrence of all species, either underestimating distribution, which was the case for *A. castelnaui* (Hozbor et al. 2004), for example, or disregarding distribution gaps, such as for *A. platana* (San Martín et al. 2007). This is not problematic if the aim is to identify the region where a species occurs, yet it may be when running ecological niche models (Sánchez-Fernández et al. 2011). The geographic distribution maps herein presented considered data of georeferenced preserved specimens and literature, and the niche models offer a simple bi-dimensional overview of the probability of occurrence of each species accounting for the abiotic conditions. Additionally, these maps can aid future assessment of conservation status for this tribe, as they comprise the data available so far on the occurrence of the four species and indicate a general set of ecological tolerances for each of them.

A remarkable advance in Natural Sciences research is the increasing cooperation towards making biological and environmental information accessible to the public. A myriad of such detailed data is currently available in free-access online databases, such as GBIF, GenBank, Bio-ORACLE and others, as well as there

being numerous tools to aid processing and analysing these data in light of biological questions (e.g. Broennimann et al. 2012). The present work takes advantage of these data and tools, and builds upon previous research by addressing knowledge gaps for a tribe of four threatened skates species. Our results contribute to a better understanding of the phylogenetic relationships of the clade Riorajini and the environmental features driving the geographic distribution of these skates in the SWA. We highlight the potential usage of currently available data to address biological questions especially for marine taxa, which are often less-studied given sampling difficulties, costly logistics and other challenges of this environment compared with on-land research.

Acknowledgements

We thank Pablo Ariel Martinez, Maria Cristina Oddone, Juan Pablo Zurano and Françoise Dantas de Lima for their valuable comments in previous versions of the manuscript.


Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

JFRC and FFP received financial support from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. SMQL receives Conselho Nacional de Desenvolvimento Científico e Tecnológico research productivity grant (313644/2018-7). FFP received financial support from the Fulbright Commission in Brazil.

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