Geographic variation in species richness, rarity, and the selection of areas for conservation: An integrative approach with Brazilian estuarine fishes

Ciro C. Vilar a, b, *, Jean-Christophe Joyeux b, Henry L. Spach c

a Programa de Pós-graduação em Ecologia e Conservação, Universidade Federal do Paraná, CP 19031, Curitiba, PR 81531-980, Brazil
b Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Av. Fernando Ferrari, Vitória, ES 29075-910, Brazil
c Centro de Estudos do Mar, Universidade Federal do Paraná, Av. Beira-Mar, Pontal do Paraná, PR 83255-976, Brazil

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A B S T R A C T

While the number of species is a key indicator of ecological assemblages, spatial conservation priorities solely identified from species richness are not necessarily efficient to protect other important biological assets. Hence, the results of spatial prioritization analysis would be greatly enhanced if richness were used in association to complementary biodiversity measures. In this study, geographic patterns in estuarine fish species rarity (i.e. the average range size in the study area), endemism and richness, were mapped and integrated to identify regions important for biodiversity conservation along the Brazilian coast. Furthermore, we analyzed the effectiveness of the national system of protected areas to represent these regions. Analyses were performed on presence/absence data of 412 fish species in 0.25° latitudinal bands covering the entire Brazilian biogeographical province. Species richness, rarity and endemism patterns differed and strongly reflected biogeographical limits and regions. However, among the existing 154 latitudinal bands, 48 were recognized as conservation priorities by concomitantly harboring high estuarine fish species richness and assemblages of geographically rare species. Priority areas identified for all estuarine fish species largely differed from those identified for Brazilian endemics. Moreover, there was no significant correlation between the different aspects of the fish assemblages considered (i.e. species richness, endemism or rarity), suggesting that designating reserves based on a single variable may lead to large gaps in the overall protection of biodiversity. Our results further revealed that the existing system of protected areas is insufficient for representing the priority bands we identified. This highlights the urgent need for expanding the national network of protected areas to maintain estuarine ecosystems with high conservation value.

A R T I C L E   K E Y   W O R D S

Brazil

C. Vilar, henny@ufpr.br (H.L. Spach).

1. Introduction

Spatial conservation strategies are often based on geographic patterns of biodiversity (Roberts et al., 2002; Brooks et al., 2006). To be effective, such strategies require spatially accurate and representative information on the distribution of biota. The lack of detailed data on geographic distribution of most biological groups, however, has not only hindered the application of methods for setting conservation priorities, but also constrained our ability to understand patterns in biodiversity. Obtaining a comprehensive measure of the spatial patterns of biodiversity is also hampered by the complexity of the concept (Purvis and Hector, 2000). For these reasons, conservation prioritization exercises often focus on univariate metrics, such as the number of species, to guide protection and restoration efforts (Brooks et al., 2006; Allen, 2008; Trebilco et al., 2011).

The total number of species (hereafter species richness) is a relatively simple and easy measure of an area's relevance to conserve biodiversity. There is solid evidence that species-rich places have increased ability to maintain key ecosystem services (e.g. food production, water quality maintenance, etc.), to recover from disturbances and to resist to invasions (Worm et al., 2006).
The local species richness, however, is only one among many attributes of biodiversity. This means that choosing areas for protection on the basis of only species richness may be inadequate to represent, for example, small-ranged and endemic species, which often have idiosyncratic geographical distributions and a high propensity to become locally rare or extinct (Roberts et al., 2002; Orme et al., 2005). Because of this, the value of spatial conservation strategies is enhanced when measures of richness are associated with complementary biodiversity metrics, such as rarity and endemism (Fleishman et al., 2006).

Using the Mexican avifauna and South American anurans as models, Villalobos et al. (2013a and b) proposed a straightforward approach to define conservation priorities at large spatial scales integrating both richness and rarity. Species considered rare because of their restricted geographic ranges also tend to have relatively small populations — two attributes that make them more prone to extinction (Roberts and Hawkins, 1999). Hence, rarity per se has been considered a double jeopardy (Gaston, 1998). Rare species often have traits distinct from those of common species and are responsible for essential — and vulnerable — ecological functions in assemblage structuring and ecosystem functioning (Mouillot et al., 2013). Conservation efforts directed to locally rare species are important even if they are common elsewhere, because they can prevent the loss of essential parts for the functioning of local ecosystems, of genetic diversity and, ultimately, extinction events (Hunter and Hutchinson, 1994; Mouillot et al., 2013).

In this study, the geographic patterns of species richness and rarity of the estuarine fish fauna were mapped and integrated to identify regions of potential conservation value on the Brazilian coast (which encompasses the whole Brazilian Province, sensu Floeter et al., 2008). We also analyzed the effectiveness of the existing system of protected areas to represent these regions. The main goal was to investigate the following questions: (1) what are the most species-rich areas for estuarine fishes? (2) where are concentrated the estuarine fish species rarer in Brazil? (3) which areas have both high estuarine fishes richness and species with relatively small geographical ranges? (4) to what extent the existing protected areas cover these crucial regions and how one might make improvements? A secondary goal was to test whether different measures of biodiversity (species richness, endemism and rarity) are spatially congruent and efficient as surrogates for each other.

2. Materials and methods

2.1. Database

A list of estuarine fish species in Brazil was compiled from (1) studies conducted in 31 estuaries distributed along the whole coast;
(2) regional checklists, identification guides, and scientific collections (references in Appendix A1). Data collection was restricted to environments that, even loosely, meet the definition of estuary proposed by Day (1980), i.e., any “partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage”. As this study focused on native estuarine species, all freshwater [i.e. of primary freshwater families sensu Berra (2007) or of the superorder Ostariophysi, except those belonging to Ariidae], oceanic and introduced species were excluded from the database, as well as those vagrant and/or of doubtful occurrence on the Brazilian coast (i.e. represented by less than three independent records). Few diadromous species occur in Brazil, including some mullets (Mugil), arid catfishes (Genidens and possibly others) and snooks (Centropomus). Since these diadromous taxa do not fit any exclusion criteria they were retained in the database. This resulted in a list with 412 fish species associated with estuaries (Table A1 in the Supplementary data), here referred to as “estuarine fishes” (lato sensu).

In a second step, the Brazilian coast was divided into 154 latitudinal bands of 0.25° (adapted from Tognelli et al., 2009), designed to provide the most detailed solutions possible given the spatial resolution of the biological data. Each species was recorded as present or absent in latitudinal bands based on geographic distribution data obtained from the “Catálogo das Espécies de Peixes Marinhas do Brasil” (Menezes et al., 2003). Because most species occur in other coastal environments besides estuaries, they were considered present in the bands (with or without estuaries) located between the endpoints of their range and absent in the others. The northern and southern limits of the species distribution along the Brazilian coast were subsequently adjusted using more accurate information, such as local species lists and guides, updated taxonomic reviews, reported range extensions, and capture locations of specimens deposited in scientific collections. The sources consulted

Fig. 2. Geographic patterns of richness considering 412 estuarine fish species (a), 28 endemic species (b) and rarity for all species (c) and for species endemic to the Brazilian coast (d). Values denote the number of species (a and b) and the average range-size (in number of bands of 0.25° occupied in Brazil) of species in each latitudinal band (c and d). Names of states mentioned in the text can be found in Fig. 1. The map on the upper left corner shows the marine biogeographical realms (sensu Spalding et al., 2007) referred to in the discussion and their transition zone on the Brazilian coast (dashed line). The bands were longitudinally extended for a better visualization.
to determine species’ ranges are listed in Appendix A2.

2.2. Analysis

For each latitudinal band we estimated (1) the total species richness, by counting all species of estuarine fishes present and (2) the rarity, calculated as the average geographic range (in terms of number of bands occupied in Brazil) of all species recorded in a particular band (Villalobos et al., 2013a). From this information, bands that have both high species richness and assemblages of relatively rare species (i.e. low average range size) were identified using an approach based on the division of values into quantiles, commonly applied to define biodiversity hotspots (e.g. Tittensor et al., 2010) and species’ rarity (e.g. Kreft et al., 2006). Following the method proposed by Villalobos et al. (2013b), the bands belonging to the fourth quartile of species richness (i.e. 25% richest) and to the first quartile of range size (i.e. 25% with lower average range size) were defined as “rich-rare”.

The analyses cited above were also performed including only 28 species endemic to the Brazilian coast (sensu Menezes et al., 2003; Floeter et al., 2008; see Table A1), because their particular distribution pattern implies that their management rely on a single country (Brazil, in this case). To define the rich-rare bands, only 119 segments containing at least one estuary inlet were considered, and 35 bands with no identified estuary were discarded (Fig. 1). The presence/absence of estuaries in latitudinal bands was checked from the literature and careful inspection of Google Earth imagery, using a virtual altitude (43 km) sufficient to identify smaller systems. Note that identified estuaries were neither quantified nor mapped due to, among other, methodological constraints outside the scope of the study. Species richness, rarity, and geographical location of rich-rare bands were mapped using ArcGIS 9.3 (ESRI, 2009).

Shapefiles of existing protected areas (PAs) were obtained from the government website (http://mapas.mma.gov.br/i3geo/datadownload.htm) to identify marine and coastal PAs, including estuaries within their limits (Fig. 1). These PAs were divided into two formal categories (integral protection, whose main goal is the protection of biodiversity, and sustainable use, which allows for some types of extractive use) and utilized to determine which bands are currently protected. In this study, all the bands with at least one PA encompassing any estuarine area were considered entirely protected. Using this definition, the efficiency of the Brazilian system of PAs to cover the rich-rare bands was determined.

Finally, to analyze the spatial congruence between richness, endemism (i.e. number of species with their ranges entirely within Brazil) and rarity, Pearson correlations were performed using the software SAM 4.0 (Rangel et al., 2010). The significance of the correlations was corrected using Dutilleul’s (1993) method, which estimates the effective degrees of freedom based on the spatial autocorrelation of data. The results of these tests indicate whether priorities for conservation identified from one of these three variables could act as surrogates for the others.

3. Results

Of the 412 estuarine fish species considered, 371 are Actinopterygii and 41 Elasmobranchii. The total number of species per latitudinal band ranged from 160 to 328 (mean ± SD = 281 ± 52 species). The species-richest bands are situated on the coast of the state of Rio de Janeiro, where 79.6% of all fish species included in this study are estimated to occur in a single band. The coast of Rio Grande do Sul (in temperate latitudes) has the lowest total richness (Fig. 2a). The number of endemic species per latitudinal band ranged from 4 to 18 (mean ± SD = 11 ± 5 species). Endemic species are concentrated in the center of the Brazilian coast (state of Bahia) and gradually become less numerous towards the country’s north and south boundaries (Fig. 2b).

The average range size within Brazil (rarity) varied little and ranged between 119 and 130 latitudinal bands (mean ± SD = 125 ± 4). The areas inhabited by species that, on average, have wider distributions were concentrated in the middle of the study area, between the states of Piauí and Espírito Santo, while the bands occupied by species with more restricted distributions were located in the states of Amapá and Pará (in northernmost region) and Rio Grande do Sul (in southernmost region) (Fig. 2c). For endemic species, rarity ranged between 78 and 123 latitudinal bands (mean ± SD = 93 ± 10). The bands occupied mainly by widespread species were situated in the states of Amapá and Pará, while the bands inhabited by endemic species with relatively restricted distribution were located mainly in the states of Bahia and Rio de Janeiro (near the center of study area) (Fig. 2d).

Geographic range size varied hugely between species (Fig. 3a and b). The vast majority of species (296 or 71.8%) occurred in more than 50% of all latitudinal bands, while a few species (54 or 13.1%) occurred in less than a quarter of the Brazilian coast. This resulted in a left-skewed frequency distribution (skewness = −0.87; Fig. 3a). A different pattern was found for endemic species since most (20 or 71.4%) of them occurred in less than 50% of the bands. Consequently, the range-size frequency distribution is right-skewed (skewness = 0.37; Fig. 3b). Seven species occurred in less than 25% of the coast (Achirus mucuri, Akko dionaea, Genidens planifrons,

Fig. 3. Frequency distribution of range-size for all species (a) and for species endemic to the Brazilian coast (b).
Gobius boekeri, Membras dissimilis, Potamarius grandoculis and Scorpaena petricola).

The bands richest in species and, at the same time, with assemblages of relatively rare species (i.e. rich-rare) are located in the states of Amapá, Pará and Rio de Janeiro (Fig. 4a), while those rich in narrow-ranged endemic species are in the states of Bahia, Espírito Santo and also in Rio de Janeiro (Fig. 4b). Sixteen out of the 119 bands containing at least one estuary have integral-protection areas, 53 have sustainable-use areas and 7 have PAs of both categories. Only 36% (or 9) of 25 rich-rare bands currently have at least one integral-protection area (Fig. 4a). For endemic species the protection level is even lower: only 7.1% (or 2) of 28 rich-rare bands are currently protected by integral-protection areas (Fig. 4b).

Geographic patterns of species richness, endemism and rarity of all species were not correlated (at $\alpha = 0.10$) to each other (Table 1). However, a negative and marginally significant ($\alpha = 0.10$) association between endemism and rarity of endemic species was detected (Table 1).

### Table 1

Pearson correlation coefficients between different components of Brazilian estuarine fish fauna. The number of degrees of freedom (between parentheses) corrected using the method proposed by Dutilleul (1993) and significance of the correlations ($^{m}$: $P > 0.10$; $^*$: $P \leq 0.10$) are also presented. Number of samples = 154 latitudinal bands.

<table>
<thead>
<tr>
<th></th>
<th>Species richness</th>
<th>Endemism</th>
<th>Rarity (all spp.)</th>
<th>Rarity (endemic)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endemism</td>
<td>0.57 ($^{m}$)</td>
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<tr>
<td>Rarity (all spp.)</td>
<td>0.40 ($^{m}$)</td>
<td>0.69 ($^{m}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rarity (endemic)</td>
<td>0.04 ($^{m}$)</td>
<td>-0.59 ($^{*}$)</td>
<td>-0.07 ($^{m}$)</td>
<td></td>
</tr>
</tbody>
</table>

Interestingly, species richness peaked on the southeast coast (21°23′–23°09’S) of Brazil rather than on the north coast, near the Equator. Although the analyses are based on a broad survey of estuarine fish fauna (see Appendix A1), this peak is located near research centers traditionally focused on taxonomy and with important fish collections (e.g. National Museum of Rio de Janeiro and Museum of Zoology of São Paulo University). Results could, then, reflect a sampling bias in areas near these institutions (Meyer et al., 2015) and a diffuse effect from false presences existing in range maps (i.e. commission errors; Rondinini et al., 2006). Nevertheless, this pattern is consistent with those previously found for coastal bony fishes (Tittensor et al., 2010; who controlled for sampling effort), reef fishes (Floeter et al., 2001; no control of sampling effort) and sharks (Lucifora et al., 2011; also without control of sampling effort). For reef fishes, the overlap of tropical and temperate species in the southeastern Brazilian coast is often considered the cause of this pattern (Moura and Sazima, 2000;...
Floeter et al., 2001; Luiz et al., 2008), which may also apply to estuarine ichthyofauna. In fact, this region coincides with the transition zone between two widely accepted biogeographical realms: the Tropical Atlantic (which extends from beyond the northern border of Brazil to Rio de Janeiro) and the Temperate South America (which extends from Rio to beyond the southern Brazilian border) (Spalding et al., 2007; Henriques et al., 2016, Fig. 2a), where many tropical and temperate fish species reach their southern and northern distribution limits, respectively (Moura and Sazima, 2000; Floeter et al., 2001). Moreover, species richness of fishes in estuaries from around the world is strongly driven by biogeographical region and temperature (Vasconcelos et al., 2015), and this is in agreement with and could explain the general pattern of richness in Fig. 2a: higher values in the tropical realm and lower in the temperate realm.

For endemic species the pattern is considerably different (Fig. 2b) since they tend to concentrate on the central coast of the country (state of Bahia). An emerging hypothesis is that such pattern represents, at least in part, a manifestation of the mid-domain effect — the increase in endemic species richness in the center of a geographical domain owing to the geometric constraints imposed by physical or physiological barriers (Colwell and Lees, 2000; see also Mora and Robertson, 2005, for an example with fish). Coincidentally, the Brazilian endemics peak is located near the center of the Brazilian Province (sensu Floeter et al., 2008), that extends from the Amazon River to Santa Catarina. In another hand, while the mid-domain effect occurs when endemic species ranges are distributed at random within a domain, an inverse border-domain effect is geometrically created for non-endemic species at political/administrative barriers (Fig. 2c). The relatively small range sizes in Rio Grande do Sul, for example, are a direct consequence of the occurrence of temperate, higher-latitude species (Ramnogaster arcuata, Oncophterus darwini, Odontesthes bonariensis, O. incisa, etc.) whose distribution extend farther southward into Uruguay and Argentina (Menezes et al., 2003). Therefore, at the extremities of the study area, political constraints restrict species distribution, raise rarity and emphasize the country’s responsibility in protecting its own biodiversity.

The spatial differences between richness and endemism (Fig. 2a and b, Table 1) have significant implications for ichthyofauna conservation. For example, they indicate that hotspots of richness have limited utility for representing fish species restricted to Brazil, whose survival depends largely, if not solely, on the country. It also reinforces the idea that reserves established exclusively based on richness tend not to cover areas where management actions are obviously required to avoid extinction (Myers et al., 2000), as has been observed globally (Roberts et al., 2002; Orme et al., 2005; Parravicini et al., 2014). In a similar way, the discrepancy between richness and rarity of all species (Fig. 2a and c, Table 1) suggests that conservation strategies based only on hotspots of diversity could overlook many geographically rare species as they occur in both rich (e.g. Rio de Janeiro) and less rich regions (e.g. Amazon region and Rio Grande do Sul; see also Roberts et al., 2002; Parravicini et al., 2014).

By considering all species and endemic species separately to set priorities, the alternatives for investment presented herein have been extended since only five (at Rio de Janeiro) of 48 rich-rare bands were selected using both datasets. More specifically, the macrotidal region influenced by the Amazon River in the states of Pará and Amapá has emerged as conservation priority from our approach considering all species (Fig. 4a). In contrast, the analysis encompassing only endemic species prioritized bands under mesotides, influenced by comparatively smaller rivers in the states of Bahia and Espírito Santo (Fig. 4b). While the former approach selected critical areas to protect widespread species that, in Brazil, are restricted to the northernmost region (e.g. Himantura schmarda, Plagioscion auratus and P. surinamensis) and also species endemic to the Amazonian coast (e.g. Akko dionae and Scarpaenidae petricola), the latter highlighted relevant sites for the conservation of Brazilian endemics inhabiting or even restricted to the central eastern coast (e.g. Achirus mucuri and Potamarius grandoculis). Globally, tidal regime strongly influences the hydrological connectivity of the estuary with the ocean and this connectivity, in turn, affects the structure of estuarine fish assemblages. Estuaries with high connectivity tend to have not only higher species richness (Vasconcelos et al., 2015), but also fish assemblages with functional traits distinct from those in less connected systems (Henriques et al., 2017). The protection of estuarine ecosystems under such different tidal regimes and connectivity levels could, therefore, safeguard a wide array of fish functional traits.

The endemic species listed above have comparatively narrow ranges (<22 bands, Fig. 3b) and are thus particularly vulnerable to extinction (Roberts and Hawkins, 1999; Roberts et al., 2002). A network of protected areas based on rich-rare bands illustrated in Fig. 4a and b would protect such species, but how effective it would be to protect the estuarine ichthyofauna in general? Our results suggest that such network could protect (in at least one site) from 85.6% (based on Fig. 4b) to 96.3% (based on Fig. 4a and b) of the Brazilian estuarine fish fauna. One of the species not included, Genidens planifrons, is endemic to the state of Rio Grande do Sul, where most (93.3%) of the species not covered by the rich-rare bands occur. This region has a low-richness fish assemblage (Fig. 2a) but is remarkably different from the rest of the country in terms of taxonomic composition (Vilar et al., 2013), and belongs to a different biogeographical realm. Thus, the protection of these biodiversity coldspots should also be considered (Vilar et al., 2015).

Lamentably, estuaries have a low global level of protection compared to other marine ecosystems (Wood et al., 2008), and Brazil is not an exception. This study demonstrates that the existing integral-protection areas are not enough to protect bands identified as priority for the conservation of ichthyofauna, particularly for narrow-ranged endemic species. Even using a “liberal” criterion for defining a band as protected (i.e. at least one PA encompassing any estuarine area, which could overestimate protection efficiency), large gaps in the system of PAs were identified along the Brazilian coast (Fig. 4). An outstanding example is the coast of the state of Bahia, where are located most of rich-rare bands for endemic species but almost no protected estuaries. These observations are consistent with the fact that estuaries represent the coastal ecosystem least protected by Brazilian integral-protection areas (~0.2% of the country’s estuarine areas), that often only cover adjacent environments (e.g. mangroves, salt marshes, coral reefs and rocky shores) (Prates et al., 2012). This reveals the urgent need to design, implement and monitor a national strategy for the conservation of these biodiverse but often neglected ecosystems.

It is obviously impracticable for a single prioritization scheme to incorporate all biodiversity attributes in order to guide the decision-making process. Thus, developing spatial conservation strategies using complementary measures and subsequently analyzing coincidences and divergences can help identify the most efficient sites to represent biodiversity as a whole (Price, 2002; Brooks et al., 2006; Devictor et al., 2010). Using species richness, endemism and rarity, as in the present study, is a pragmatic and integrative approach to guide the allocation of resources and the delimitation of PAs at smaller spatial scales (e.g. within the rich-rare latitudinal bands). For the delimitation process we emphasize that taking into account social, economic and management constraints can help to translating conservation planning into protection actions. While a broad stakeholder engagement would be necessary before implementation of our results, this study
provides an important first step to conserving estuarine ecosystems with high biological relevance and used by thousands of people.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2017.06.022.

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ESRI (Environmental Systems Research Institute), 2009. ArcView GIS Ver. 9.3.1.