Adriana Marcela Morales Guerrero

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Índice

Capítulo 1

Introdução Geral

Áreas de endemismo: definição e delimitação

Uma área de endemismo ou elemento biótico é uma região geográfica que apresenta congruência distribucional entre táxons (Morrone, 2014), gerada por processos históricos ou ecológicos (Platnick, 1991; Harold & Mooi, 1994; Linder, 2001; Morrone, 2014; Szumik & Goloboff, 2004). Áreas de endemismo são as menores unidades de análise da biogeografia histórica e, como tal, são a base para construção de hipóteses sobre os processos responsáveis pela formação da biota de uma região (Morrone, 2001). Portanto, áreas de endemismo são hipóteses testáveis e modificáveis com a inclusão de novos dados de distribuição (Carvalho, 2011). Diversos métodos para o reconhecimento de áreas de endemismo têm sido empregados. Os métodos atualmente mais utilizados são a análise de Parcimônia de Endemicidade (PAE, Morrone, 1994) e a Análise de Endemicidade (EA, Szumik *et al.,* 2002; Szumik & Goloboff 2004), que calcula o valor de endemicidade mediante alguns critérios (Aagesen, *et al.,* 2009; Navarro, *et al.,* 2009; Szumik *et al.,* 2012; Casagranda *et al.,* 2012; Prado *et al.,* 2014; Martínez-Hernández *et al.,* 2015; Noguera-Urbano & Escalante, 2015).

A análise de três-itens (3IA, Nelson & Platnick, 1991) é uma metodologia de inferência filogenética que utiliza a mínima expressão hierárquica possível (3is- enunciados de três-itens) para encontrar padrões relacionais (Williams & Siebert, 2000; Williams & Ebach, 2005). A análise de parcimônia padrão e a 3IA aplicam o mesmo critério de otimização, porém utilizam matrizes de dados diferentes: binária e de 3is, respectivamente, que resolvem diferentemente os caracteres conflitantes (Platnick, 1993; Nelson, 1996; Williams, 2002). A 3IA tem sido uma metodologia geralmente utilizada para inferir *relações* entre áreas de endemismo (Nelson & Platnick, 1991; Roig-Juñent *et al.,* 2006; Escalante *et al.,* 2007; Parenti & Ebach, 2009). Porém, sob uma perspectiva prática, e a despeito de ser uma opção que aparentemente incorpora a incerteza dos dados de distribuição nas entradas faltantes (Marques, 2005), enunciados de três-itens não foram explorados para a análise de congruência distribucional entre táxons ou homologia biogeográfica primária (senso Morrone, 2001).

Abertura do Oceano Atlântico Sul-Ocidental

Atualmente, a Biogeografia Marinha está frequentemente concentrada na caracterização de congruência distribucional entre táxons (e.g., Glasby & Alvarez, 1999; Moreno *et al*., 2006; Marques & Peña Cantero, 2010; Miranda, *et al*., 2015). Estudos comparando diferentes metodologias aplicadas na definição de áreas de endemismo marinhas são incipientes (Vargas *et al*., 2008). Essa inexistência de estudos em biogeografia para a maioria dos grupos marinhos pode ser creditada ao fato de que a ideia de que "Terra e vida evoluem juntas", cunhada por León Croizat (1964), não é tão evidente no meio marinho. Além disso, os ciclos de vida das espécies marinhas são pouco explorados, embora de suma importância para a compreensão da evolução no tempo e espaço (Miranda, *et al*., 2011).

O Oceano Atlântico Sul-Ocidental (OASO), uma extensa linha de costa que inclui diversos ecossistemas e domínios de paisagem, estende-se ao longo da costa sul do Brasil pelas costas do Uruguai e Argentina. A abertura e o surgimento do Oceano Atlântico Sul teve início após a separação da Pangeia, durante a fase de fragmentação da Gondwana, ao final do Triássico e início do Jurássico (Lavina & Fauth, 2011). Durante afastamento das placas de formação do Atlântico, produziu-se alguns regimes e frentes oceânicas (Piola *et al.*, 2000; Acha *et al.*, 2004; Lucas *et al.*, 2005; Miranda & Marques, 2011), como as ressurgências de Cabo Frio e do Cabo de Santa Marta Grande, os estuários da Lagoa dos Patos, do Rio de la Plata, de Rincón (na Península Verde, um acidente geográfico do litoral Argentino), as frentes de marés da Península de Valdés e do Talude Argentino, e a frente frio do estuário da Patagônia. Hoje compreende-se que esses regimes e frentes podem agir como barreiras biogeográficas no OASO por possuírem forte influência sobre a estrutura populacional de suas espécies (Galarza, *et al.*, 2009). Outras barreiras biogeográficas podem ser diferenças de temperatura, salinidade, profundidade, densidade, composição de fundo e a interface de água com o ar (Acha *et al.*, 2015).

Segundo alguns padrões de congruência distribucional entre táxons (especialmente em peixes), o OASO inclui quatro regiões biogeográficas: Antártida, Temperado-Quente, Temperado-Frio, Tropical (Briggs, 1995; Bailey, 1998; Briggs & Bowen, 2012, 2013; Servais *et al.*, 2013). De maneira similar, Spalding *et al.* (2007) dividiram o OASO em duas províncias

(Atlântico Sudoeste Temperado-Quente e Magalhânica) e oito ecorregiões, Sudeste do Brasil, Rio Grande, Rio de la Plata, Plataforma Uruguai-Buenos Aires, Golfo do Patagônia, Plataforma da Patagônia, Falklands/Malvinas e canais e fiordes do sul do Chile, suportadas por diferentes eventos históricos ou ecológicos.

Hidrozoários na biogeografia marinha

Cnidários caracterizam-se pela presença de cnidas (Marques & Collins 2004), organelas urticantes usadas na alimentação, defesa, locomoção e fixação. Suas espécies são encontradas em ambientes pelágicos e bentônicos, com limites de distribuição relacionados a condições abióticas (*e.g.*, limites de salinidade, temperatura) e bióticas (*e.g.*, ecológicas). Cnidários podem possuir ciclo de vida complexo, envolvendo duas fases, pólipo (geralmente fixo) e medusa (geralmente livre natante), com variações sobre este ciclo básico. Apresentam particularidades importantes para estudos evolutivos, relacionadas à sua biologia e história de vida complexa e por possuírem uma posição basal na evolução animal (Marques *et al.*, 2003; Marques & Collins 2004; Collins *et al.*, 2006, 2008; Cartwright *et al.*, 2008). Em Medusozoa (linhagem cujo ancestral tinha a fase de medusa em seu ciclo de vida), a classe Hydrozoa é a mais rica e diversa (~3.800 espécies, Schuchert, 2015). Hydrozoa têm grande importância no bentos e plâncton marinhos devido ao seu crescimento rápido (reprodução assexuada), seu pioneirismo na colonização de substratos naturais e artificiais, e sua enorme diversidade de estratégias em seu ciclo de vida (*cf.* Boero & Bouillon *et al.*, 1993; Migotto *et al.*, 2001; Genzano *et al.*, 2003; Bouillon *et al.*, 2006).

Estudos de biogeografia marinha no OASO com Hydrozoa são escassos. Recentemente foi publicado um estudo sobre a distribuição de 130 espécies de hidroides bentônicos da região entre 22°-55°S, em que foram encontrados três padrões principais de áreas de endemismo: Tropical, Subtropical e padrões disjuntos entre estes dois (Miranda *et al.*, 2015). Outros estudos biogeográficos com a distribuição de hidroides bentônicos no Oceano Atlântico (OA) e áreas adjacências são Medel & López-González (1998), Marques & Peña Cantero (2010) e Miranda *et al.* (2013). Finamente, Gibbons *et al.* (2010), usando diferentes estratégias do ciclo de vida em Hydrozoa, demonstraram que espécies holoplanctônicas têm menor estrutura biogeográfica que espécies meroplanctônicas, as quais têm menor estrutura que espécies bentônicas (Gibbons *et al.*, 2010).

Objetivos gerais do estudo

Nesta dissertação, propomos uma comparação integrada de alguns dos métodos mais utilizados em análises de endemismo, *viz.*, PAE (Morrone, 1994) e EA (Szumik *et al.*, 2002; Szumik & Goloboff, 2004), comparando-os com a Análise de Distribuições de três-itens (3ID). No **Capítulo 2** avaliamos 43 conjuntos de dados hipotéticos buscando fornecer uma ampla compreensão do desempenho dos algoritmos e as consequências da sua aplicação em conjuntos de dados de configurações diferentes. No **Capítulo 3**, foram compiladas 214 espécies de Hydrozoa incluindo as três principais estratégias de ciclo de vida, visando esclarecer a história biogeográfica da diversificação do táxon e analisar os padrões de distribuição no ambiente bentônico, pelágico e bentopelágico do OASO. Outros objetivos do estudo foram testar hipóteses anteriores de regionalização do OASO (*viz.*, Spalding *et al.*, 2007; Briggs & Bowen, 2012, 2013; Miranda et al, 2015) e analisar o desempenho dos métodos com conjuntos de dados reais.

Organização da dissertação

A dissertação é apresentada em quatro capítulos. O **Capítulo 1** contém a introdução geral, a qual expõe as características principais do estudo, seus objetivos e sua forma de organização. Os **Capítulos 2** e **3** são apresentados na forma de artigos científicos com introdução, objetivos, resultados e discussões específicos e independentes de cada um, porém relacionados em um contexto maior.

O **Capítulo 2,** intitulado “Comparison of analysis of endemism procedures based on hypothetical distributions” apresenta uma avaliação do desempenho dos métodos de análise de endemismo (*viz.*, PAE, EA e 3ID) com base na capacidade dos métodos para identificar padrões de endemismo em cenários predefinidos. Os resultados deste estudo mostram que 3ID tem o maior percentual de sucesso na recuperação de padrões predefinidos. Igualmente, EA é o único método que resolve completamente padrões de áreas de endemismo sobrepostas. Neste capítulo, portanto, sugerimos que a melhor opção em uma análise de endemismo, é o uso de 3ID e EA em conjunto.

No **Capítulo 3**, intitulado “Biogeographic patterns of benthic and planktonic hydrozoans from the southwestern Atlantic Ocean”, dados de 214 espécies de Hydrozoa do Oceano Atlântico Sul-Ocidental foram analisados por meio da PAE, EA e 3ID, considerando as diferentes estratégias dos ciclos de vida em Hydrozoa. Os resultados deste estudo mostram três padrões gerais de endemismo: (1) Tropical (2) Temperado-Quente, e (3) Temperado-Frio, todos concordantes com hipóteses biogeográficas anteriores para a região de estudo. Igualmente, os padrões obtidos variam de acordo com o tipo de ciclo de vida em Hydrozoa, demonstrando a importância de analisar-se separadamente conjuntos de dados de espécies com diferentes estratégias de reprodução.

Por fim, o **Capitulo 4** traz as considerações finais desse estudo, destacando e concatenando os principais resultados obtidos nos capítulos anteriores.

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Capítulo 2

Comparison of analysis of endemism procedures based on hypothetical distributions

Adriana Morales-Guerrero [1], Thaís P. Miranda [1] and Antonio C. Marques[1,2]

[1] *Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, Brazil,*

[2] *Center for Marine Biology, University of São Paulo, São Sebastião, São Paulo, Brazil.*

ABSTRACT

Areas of endemism are identified in a variety of ways, with no universally accepted standard. Performance of each method will depend upon the variables chosen. Here, we compare Parsimony Analysis of Endemicity (PAE), Endemicity Analysis (EA) and a new coding method that we propose, Three-Item Analysis of Distributions (3ID). We determine performance based on ability to identify hypothetical predefined patterns that represent non-conflicting, nested and overlapping areas of endemism. Additionally, properties commonly used in analyses, such as shape and size of the area and the number of taxa involved, were also compared. We found that 3ID has the greatest percentage of success in retrieving predefined areas. EA is the only method that resolved a completely overlapping pattern, but it also found spurious patterns. PAE always resolved with less precision and efficiency and so is not the best option for analysis of endemism. We recommend the use of 3ID together with EA as the best available option for hypothesizing areas of endemism.

RESUMO

Áreas de endemismo podem ser identificadas por uma série de métodos, não havendo um padrão metodológico definido e aceito universalmente. O desempenho de cada método usado irá depender das variáveis escolhidas e do conjunto de dados analisado. Nós comparamos a Análise de Parcimônia de endemicidade (PAE), a Análise de Endemicidade (EA) e um novo método de codificação que propomos a Análise de Distribuições de três-Itens (3ID), determinando o desempenho dos métodos com base na capacidade de identificar padrões hipotéticos predefinidos de áreas de endemismo, representando áreas não conflitantes, aninhadas e sobrepostas. Além disso, foram comparadas propriedades comumente usadas nas análises, como a forma e tamanho das áreas e o número de táxons envolvidos nas análises. Os resultados mostram que a 3ID tem o maior percentual de sucesso na recuperação de áreas de endemismo predefinidas. Adicionalmente, a EA é o único método capaz de resolver completamente um padrão sobreposto, porém também pode encontrar padrões espúrios. A PAE sempre obteve a menor precisão e eficiência na recuperação das áreas predefinidas e, portanto, não é a melhor opção para análises de endemismo. Sugerimos que o uso de 3ID e EA em conjunto é a melhor opção para buscas e delimitação de áreas de endemismo.

Key words: Three-Item Analysis of Distributions, Parsimony Analysis of Endemicity, Endemicity Analysis, areas of endemism, Biogeography

INTRODUCTION

Areas of endemism comprise regions in which more than one taxon is found with similar distributional patterns (Morrone, 1994). Origins or causes of areas of endemism are consequences of barriers due to historical or ecological factors that result in isolation of a given biota during a certain period of time (Harold & Mooi, 1994; Morrone, 2014). Areas of endemism are considered to be basic units of analysis in the field of Historical Biogeography (Cracraft, 1985; Crother & Murray, 2011).

In practice, criteria for analysing or determining areas of endemism are subject to debate. Areas of endemism are traditionally defined as the distributional congruence of two or more taxa with a cohesive response (= synapomorphic traits) to ecological or historical changes (Platnick, 1991; Harold & Mooi, 1994; Linder, 2001; Morrone, 2014). Alternatively, it has been suggested that areas of endemism could be diagnosed by a single species (Humphries & Parenti, 1999; Crother & Murray, 2011) or by forming a monophyletic group (Harold & Mooi, 1994).

Hypotheses of areas of endemism are inferred in several ways, such as 1) phylogenetic patterns of primary biogeographic homology based on parsimony algorithms (Parsimony Analysis of Endemism, PAE, Morrone, 1994; and derivations, CADE, Porzecanski & Cracraft, 2005; PAE-PCE, Luna-Vega *et al.*, 2000; AoE, Deo & DeSalle 2006), 2) congruence between species distribution using Endemicity Analysis (EA, Szumik *et al.*, 2002; Szumik & Goloboff, 2004), 3) Network Analysis (NAM, Dos Santos *et al.*, 2008), 4) analysis of biotic elements based on distance measurements (Hausdorf & Hennig, 2003) and 5) analysis of spatial interpolation (Oliveira *et al.*, 2015), among others. A first step in all procedures is to build the data matrix. Classical matrices of endemicity analyses include putative groups among distributions that are placed in columns (components, sensu Nelson, 1979). Locations are rows, in which each component is coded for presence (1) or absence (0). Subsequently, PAE infers areas of endemism by the fewest number of changes and not by relationships (Williams & Ebach, 2006), and EA infers areas of endemism by the criteria of the Endemicity Index (EI). An alternative treatment for the data matrix is transformation of the original components into statements of three items (Three-Item Analysis, 3IA). Three-Item Analysis does not consider character states in a transformation series for distributional data, but rather character states are expressed as the minimum statement of relationships (three-item statements) and hierarchical patterns minimize the misfit of these statements (Nelson & Platnick, 1991; Delaporte, 1996). This method has proven to be more efficient when compared to other binary codings because the statements better represent the data (Nelson & Platnick, 1991; Williams, 2002; Nelson *et al.*, 2003), and because the consistency of using the initial hierarchical structure for a final hierarchical result (Cao *et al.*, 2007).

Theoretical and operational grounds of 3IA have been widely discussed (Nelson & Platnick, 1991; Platnick *et al.*, 1996; Williams, 2002; Nelson *et al.*, 2003; Marques, 2005; Williams & Ebach 2005, 2006; Cao *et al.*, 2007). Used as a method to infer *relationships* between areas of endemism (Nelson & Platnick, 1991; Roig-Juñent *et al.*, 2006; Escalante *et al.*, 2007; Parenti & Ebach, 2009: 170-186), 3IA statements of three distributions have not yet been explored for primary biogeographic homology analysis. However, observations incorporated into binary matrices include uncertainties or errors (e.g., incompleteness of sampling taxa, extinction) that may result in misguided indications of patterns (Marques & Gnaspini, 2001; Marques, 2005). Using matrices that encode the smallest statements of comparison, in which uncertainty is included by using missing entries (Marques, 2005), may provide a more efficient model for analyses of endemism.

Comparisons of PAE and EA with real (Szumik *et al.*, 2002; Moline & Linder, 2006; Carine *et al.*, 2009; Escalante *et al.*, 2009; Da Silva *et al.*, 2015; Escalante, 2015) and hypothetical data sets (Casagranda *et al.*, 2012) have been published. Real datasets provide limited assessment of methodological nuances and their results may be affected by distributional idiosyncrasies and properties of the methods. Casagranda et al. (2012) analyzed four cases of hypothetical distributions and different degrees of sympatry between taxa. However, there is an unlimited universe of these patterns that allow us the comparative analysis between methods. Thus, it is possible to evaluate many scenarios and perform deeper comparisons of analyses of endemism.

In this study, we examine the strengths and weaknesses of the most-commonly used methods in analyses of areas of endemism: PAE (Morrone, 1994) and EA (Szumik *et al.*, 2002; Szumik & Goloboff, 2004). We then compare them to Three-item Analysis of Distributions (3ID). We compared methods by using hypothetical datasets designed to recreate specific distribution patterns. Our unique approach uses 3ID to hypothesize areas of endemism and then explains performance of the algorithms and the consequences of their application to data sets with different configurations.

METHODS

Data sources

Endless possibilities with different and conflicting distribution patterns can arise in any data matrix and, while some conflicting patterns between species are often obvious to the eye, resolving them is not a trivial algorithmic process. We designed 43 hypothetical distribution patterns framed in three general patterns: 1) non-conflicting (strict sympatry between the areas, sensu Platnick, 1991), 2) overlapping (two or more areas are partially overlapped) and 3) nested (a smaller area is nested into a larger area, Fig. 1). We analyzed five types of overlapping patterns (Fig. 2) and two types of nested patterns (Fig. 3) while managing the following variables: area size, number of taxa per area, and change in shape of distributions (Appendix 1). All generated patterns used a range of eight to 16 species in a spatial matrix of 36 cells, with 6° latitude and longitude (Table 1).

Algorithmic procedures

The 43 hypothetical distribution patterns were analyzed using EA (Szumik *et al.*, 2002; Szumik & Goloboff, 2004), PAE (Morrone, 1994), and 3ID. EA was carried out for a binary matrix applying the heuristic algorithm of NDM-VNDM version 3.0 (Goloboff, 2011), using the default parameters. Cells were swapped one at a time and the search was repeated 1,000 times. The PAE used a binary matrix and 3ID a three-item matrix with fractional weights (Nelson &

Ladiges, 1992) generated by TAXODIUM 1.0 (Mavrodiev & Madorsky, 2012). Both matrices were analyzed with the software TNT version 1.1 (Goloboff *et al.*, 2008), using a heuristic search with TBR and 1000 Wagner trees with random addition sequences (mult/1000). Ten cladograms for each run (Hold/10) were kept and the results were summarized by strict consensus.

Evaluation criteria

We evaluated the performance of the methods by two indices that quantify the congruence between identified and predefined patterns: the sensitivity and the specificity indexes (Casagranda *et al.*, 2012). The sensitivity index is the proportion of cells within a predefined pattern that is correctly identified by the method, *i.e.*, **I_{Sens}=TP/Predefined**, in which TP (true positives) is the number of cells found in identified patterns corresponding to the predefined pattern. I_{Sens} varies between 0 (identified pattern includes none of the cells of the predefined patterns) to 1 (identified pattern is identical to the predefined pattern).

The specificity index is the proportion of cells within an identified pattern that are included in a predefined pattern, *i.e.*, **I_{Spec}=TP/Identified.** Values for I_{Spec} vary between 0 (identified pattern includes none of the cells of the predefined pattern) and 1 (identified pattern includes all cells of the predefined pattern). I_{Spec} decreases when the identified pattern includes a number of false positives (FP), *i.e.*, cells present in the identified pattern but not in the predefined one.

Each identified pattern was placed in one of four categories defined according to their I_{Sens} and I_{Spec} values: (a) correctly identified patterns (I_{sens} and $I_{spec} \geq 0.9$), (b) partially identified patterns ($I_{sens} < I_{spec}$), (c) over-identified patterns ($I_{sens} \geq I_{spec}$) and (d) incorrectly identified patterns (I_{sens} and $I_{spec} \leq 0.5$).

RESULTS

The following patterns were found using sensitivity and specificity indices of each area of endemism:

Non-conflictive patterns. EA, PAE and 3ID recovered 100% of the predefined areas.

Overlapping patterns. From the 103 predefined areas, EA correctly recognized only 48 (47%), partially identified 4 (4%) and over-identified another 29 (28%), for a total of the 81 identified areas (78%). PAE correctly recovered 60 (58%) and 3ID 72 (70%) areas (Fig. 4). EA frequently fails to find overlapping patterns due to extra or missing cells in the patterns. Also, hierarchical methods never recognize two overlapping areas together, but rather only recover one of the two.

Nested patterns. From the 45 predefined areas, EA correctly identified 27 (60%), PAE correctly identified 36 (80%) and 3ID correctly identified 38 (84%) areas (Fig. 5). In this case, PAE and 3ID recovered strict sympatry or homopatry more successfully, while EA sometimes failed. None of the methods were successful in recognizing nested areas that have two internal overlapping patterns with the same number of species, area size, and shape of distributions (*e.g.*, hypothetical distribution 43 in Appendix 1).

DISCUSSION

Only *Endemicity Analysis* (EA) perfectly identified the pair of overlapping areas, yet it had the poorest performance in finding nested patterns (60%), in addition to being the only method that found spurious patterns (over-identified, Fig. 4). The over-identified patterns (areas with extra cells in addition to those of the predefined patterns) found by EA were a consequence of the evenness rule of the NDM algorithm. Due to this rule, a species absent in one cell but present in adjacent cells can be considered to be present (Szumik & Goloboff, 2004). To include distributional uncertainties, it is important to hypothesize maximum areas of endemism because the absence of a species in a given area may for several reasons, including insufficient collecting effort. However, depending on the dataset and the available evidence of distribution, an inferred congruence between cells that, in fact, lack any relationship may occur (artifact). The NDM consensus option may reduce the influence of these artifacts (Casagranda *et al.*, 2012, Aagesen *et al.*, 2013), but, this may only be applicable if some areas share similar numbers and composition of species. However, some areas are the only result from a group of species and, therefore, to apply the consensus rule for these cases is not possible (Appendix 1, results of the analyses of hypothetical distributions 14, 19, in blue, and 24, in gray).

A common result of EA is that areas with over-identified cells have lower endemicity score than areas in which cells without species were eliminated and therefore areas with low-score could be removed (Szumik & Goloboff, 2004). We find, however, that this does not always occur and in eight out of 14 (57%) hypothetical patterns, over-identified areas did not have lower scores in relation to other areas (Fig. 6). This is because over-identified areas may be the only result for a group of species and thus, neither consensus rule of EA nor removing areas with the lowest scores are efficient alternatives to eliminate the methodological artifact from the analysis.

Parsimony Analysis of Endemicity (PAE) performs poorly in identifying overlapping areas (Casagranda et al. 2012), with results that are intermediate between 3ID and EA (Fig. 4). However, outcomes from PAE may improve when areas have different number of species. Improved performance also involved nested noise (80%), yet outcomes are better using 3ID among hierarchical methods (84%, Fig. 5).

Three-item Analysis of Distributions (3ID) includes matrices coded with the smallest statement of distributions (3ID), and had greater success rates in recovering predefined cells. 3ID also performed better in retrieving nested areas, followed by PAE and then EA. This rank order suggests that hierarchical methods are better at solving nested information (Escalante 2015). Indeed, applying the consensus option in EA when analysing nested areas removes the few nested patterns that EA detected. Yet, 3ID is unable to retrieve pairs of overlapping areas of the same size with the same number of species, but performance improves when areas have different number of species or areas have different dimensions (in these cases retrieve one overlapping area). Indeed, 3ID recovered areas with different dimensions, because of the use of fractional weights for each statement. In so doing, the larger number of presences of a given taxon increases the number of statements of three distributions and, therefore, decreases their fractional weights (Nelson & Ladiges, 1992). This explains how 3ID retrieves at least one overlapping area and prefers areas not supported by widespread species.

In conclusion, here we demonstrate that performance varies widely by algorithm in the identification of different patterns of areas of endemism, and that they may find spurious patterns due to methodological flaws and artifacts. We show how performance depends on variables such as the geographical shape and size of the area, and number of taxa. Still, the importance of other variables remains to be explored, including sample size, sampling biases, and so on. We used simple hypothetical examples and found that they provide a powerful option to evaluate the performance of the methods. This allowed us to avoid complexities generated by simultaneous variables presented in real datasets. The decision of which method should be applied may not be universal, and the conditions themselves can influence performance of the method used to identify areas of endemism. Based on our experiments, using 3ID and EA together is the best available option to identify areas of endemism, because together they avoid problems caused by over-identified patterns and missing information in overlapping or nested areas.

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FIGURES AND TABLES

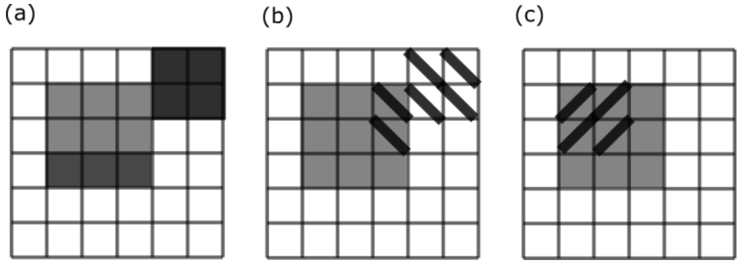


Figure 1. Hypothetical distributions to illustrate use in the simulations. (a) Non-conflicting patterns: three contiguous areas of endemism, each defined by a particular set of endemic species, *i.e.*, strict sympatry. (b) Overlapping areas: two spatially overlapping areas of endemism, each defined by a particular set of endemic species. (c) Nested areas: a small area of endemism defined by its endemic species set is nested into a larger area defined by another set of endemic species which include the set of species in the smaller area of endemism.

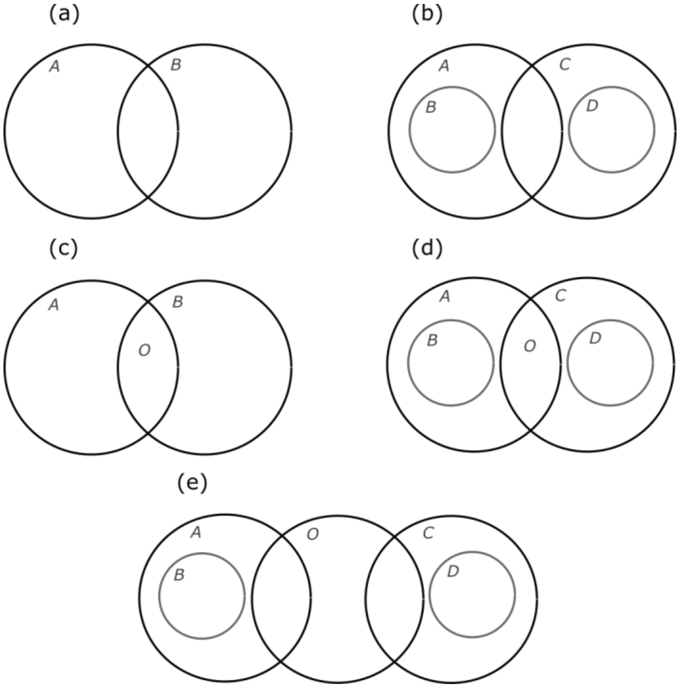


Figure 2. Overlapping patterns evaluated in this study. (a) Type I: two predefined areas: A and B. (b) Type II: four predefined areas: A, B, C and D. (c) Type III: three predefined patterns: A, B and O. (d) Type VI: five predefined areas: A, B, C, D and O. (e) Type V: five predefined areas: A, B, C, D and O (Table 1).

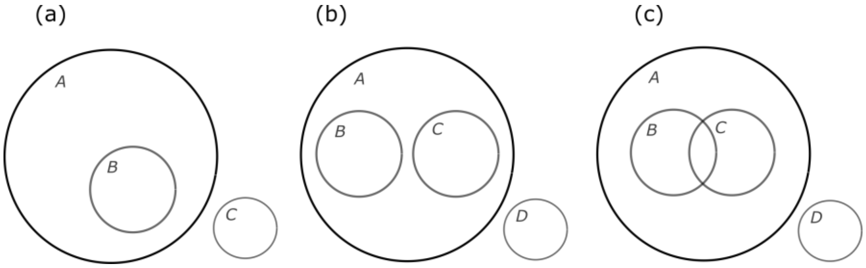


Figure 3. Nested patterns evaluated in this study. (a, b) Type I: three predefined patterns: A, B and C. (c) Type II: four predefined patterns: A, B, C and D (Table 1 and Appendix 1).

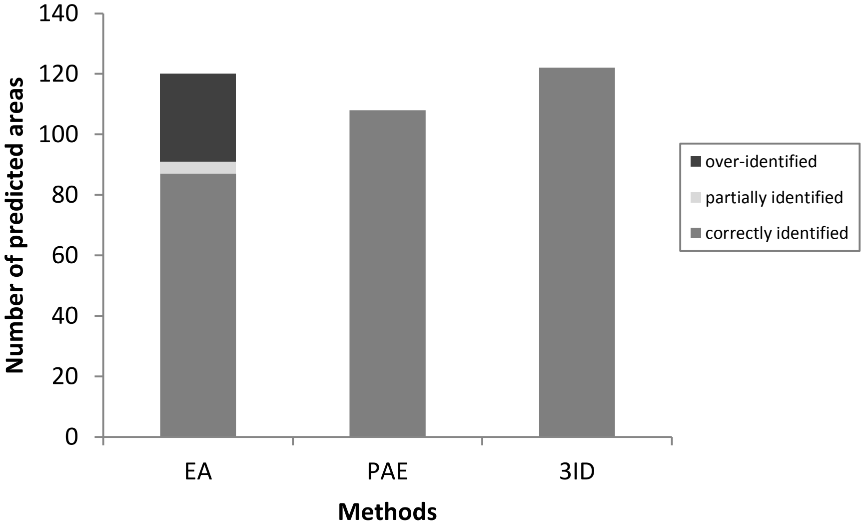


Figure 4. Number of correct (dark grey), partial (pale grey), and over-identified (black) areas recovered by each method of the analysis of the 27 overlapping patterns (103 predefined areas).

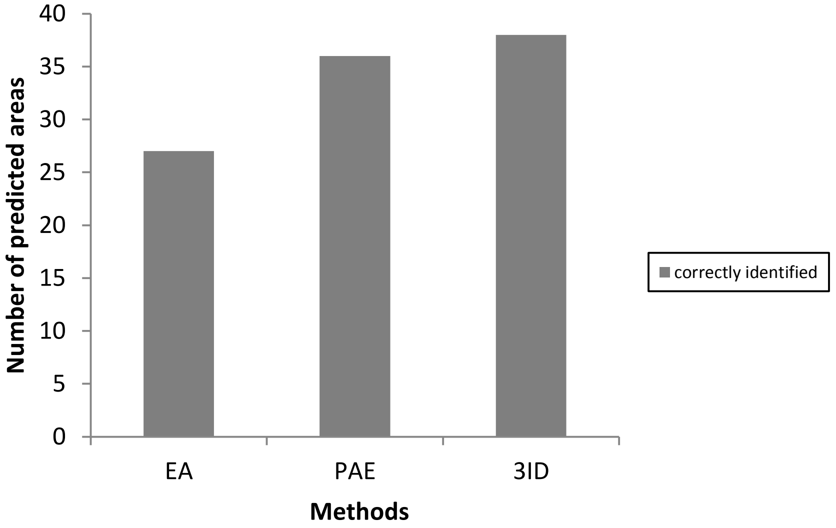


Figure 5. Number of correct areas recovered by each method in the analysis of 12 nested patterns (45 predefined areas).

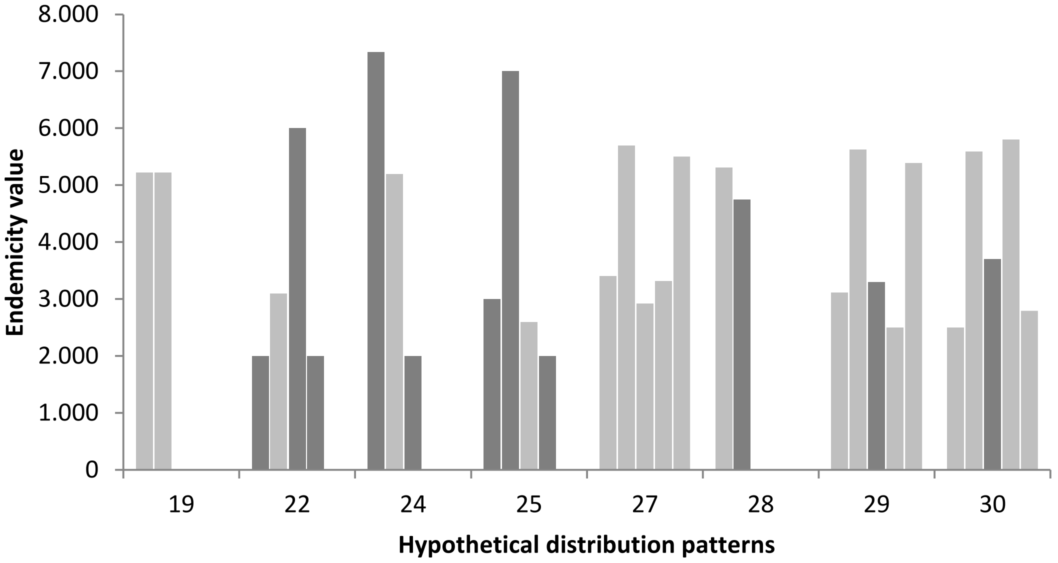


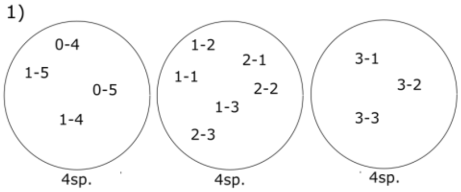
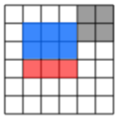
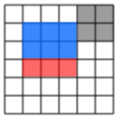
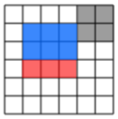
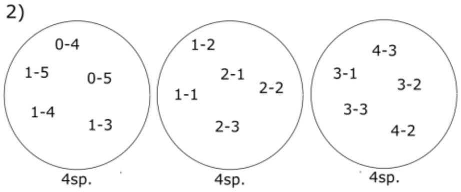
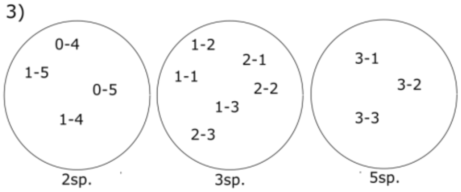
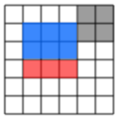
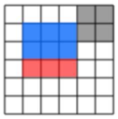
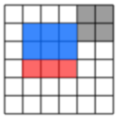
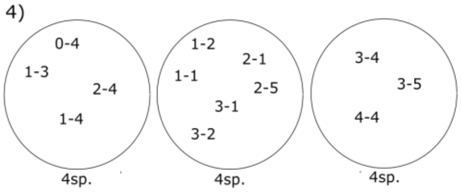
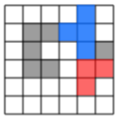
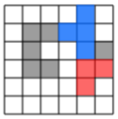
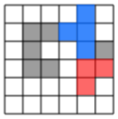
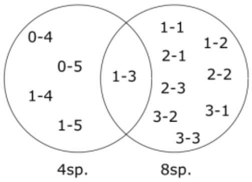
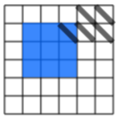
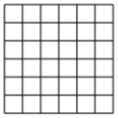
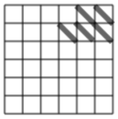
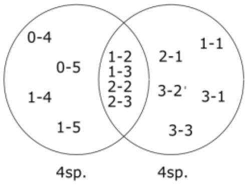
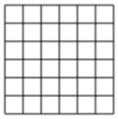
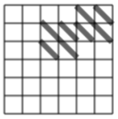
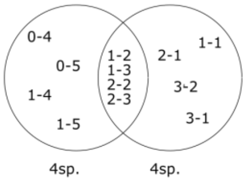
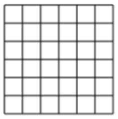
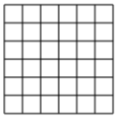
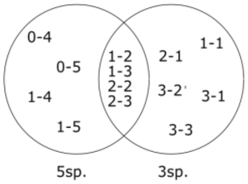
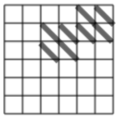
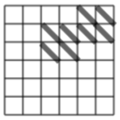
Figure 6. Endemicity value for each correct (dark grey), and over-identified (pale grey) area found by eight hypothetical distributions using EA.

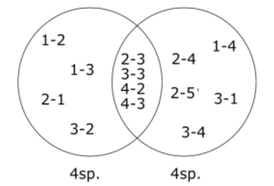
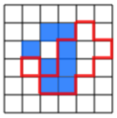
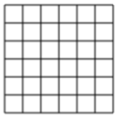
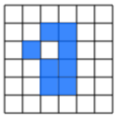
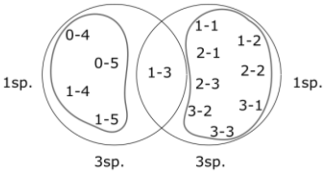
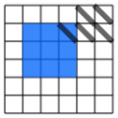
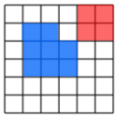
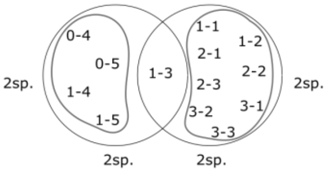
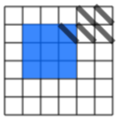
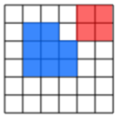
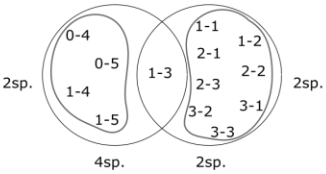
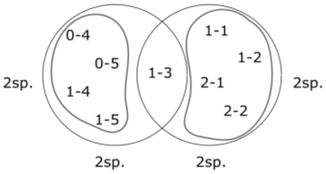
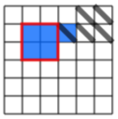
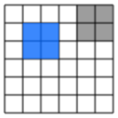
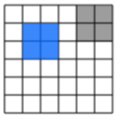
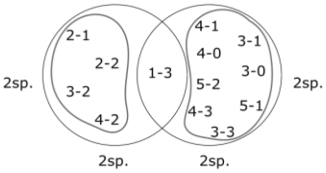
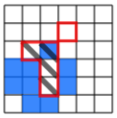
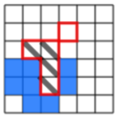
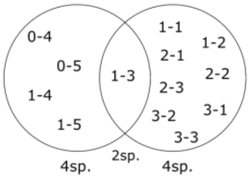
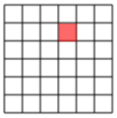
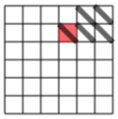
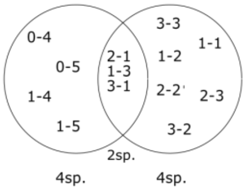
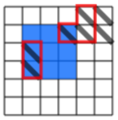
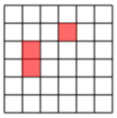
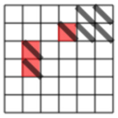
Table 1. Details of hypothetical examples with the list of cases, the number of endemic species per area, the size of each area and the sum of resulting areas by case. The hypothetical distributions are organized as A=X:Y, where A is the identified area of endemism, X the number of endemic species of the area, and Y the size of the area (number of cells occupied by each area); O are complementary areas; s1 and s2 are different distribution shapes.

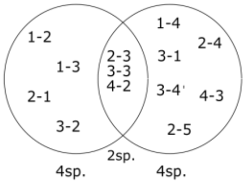
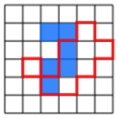
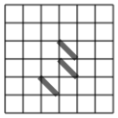
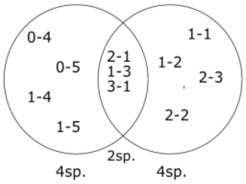
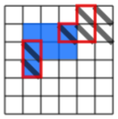
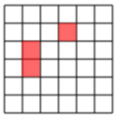
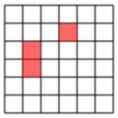
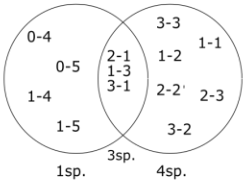
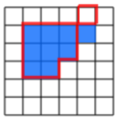
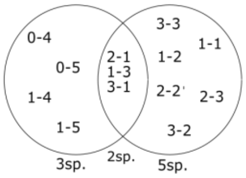
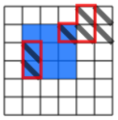
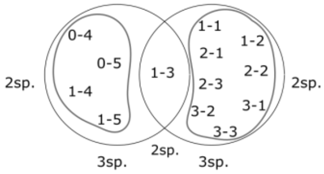
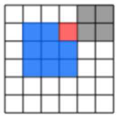
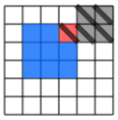
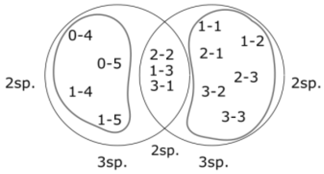
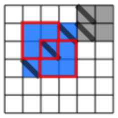
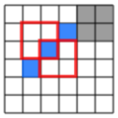
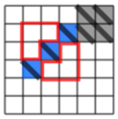
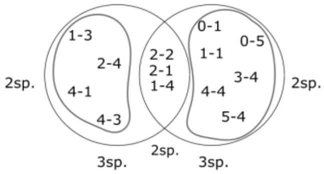
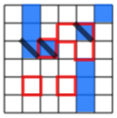
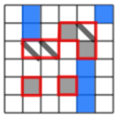
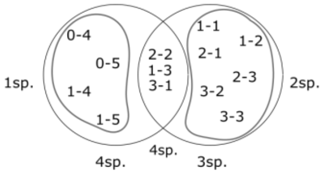
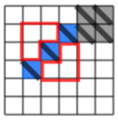
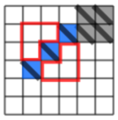
Patterns	Number of endemic species and size of the area	Sum of resulting areas by case
Non-conflicting patterns	A=4:4, B=4:6, C=4:3, s1; A=4:4, B=4:4, C=4:4; A=2:4, B=3:6, C=5:3; A=4:4, B=4:6, C=4:3, s2	12
Overlapping type I	A= 4:5, B=4:9, O=0:1; A=4:8, B=4:9, O=0:4, s1; A=4:8, B=4:8, O=0:4; A=5:8, B=3:9, O=0:4; A=4:8, B=4:9, O=0:4, s2	10
Overlapping type II	A=3:5, B=1:4, C=3:9, D=1:8, O=0:1; A=2:5, B=2:4, C=2:9, D=2:8, O=0:1, s1; A=4:5, B=2:4, C=2:9, D=2:8, O=0:1; A=2:5, B=2:4, C=2:5, D=2:4, O=0:1; A=2:5, B=2:4, C=2:9, D=2:8, O=0:1, s2	20
Overlapping type III	A=4:5, B=4:9, O=2:1; A=4:7, B=4:9, O=2:3, s1; A=4:7, B=4:9, O=2:3, s2; A=4:7, B=4:7, O=2:3; A=1:7, B=4:9, O=3:3; A=3:7, B=5:9, O=2:3	18
Overlapping type IV	A=3:5, B=2:4, C=3:9, D=2:8, O=2:1; A=3:7, B=2:4, C=3:9, D=2:6, O=2:3 s1; A=3:7, B=2:4, C=3:9, D=2:6, O=2:3 s2; A=4:7, B=1:4, C=3:9, D=2:6, O=4:3; A=2:7, B=3:4, C=4:9, D=2:6, O=2:3; A=3:7, B=2:4, C=3:7, D=2:4, O=2:3	30
Overlapping type V	A=3:6, B=2:4, C=3:8, D=2:6, O=2:2, s1; A=3:6, B=2:4, C=3:8, D=2:6, O=2:2, s2; A=3:6, B=2:4, C=3:6, D=2:4, O=2:2; A=2:6, B=3:4, C=4:8, D=1:6, O=2:2; A=5:6, B=2:4, C=2:8, D=2:6, O=2:2	25
Nested type I	A=7:8, B=3:5; A=7:8, B=3:5, C=3:3; A=7:8, B=3:5, C=3:3, D=3:3, s1; A=2:8, B=5:5, C=3:3, D=2:3; A=5:8, B=3:5, C=4:3, D=3:3; A=7:8, B=3:5, C=3:3, D=3:3, s2; A=7:6, B=3:3, C=3:3, D=3:3	25
Nested type II	A=6:8, B=3:6, C=3:5, O=0:3, D=3:3, s1; A=4:8, B=4:6, C=2:5, O=0:3, D=3:3; A=4:8, B=2:6, C=4:5, O=0:3, D=3:3; A=6:8, B=3:6, C=3:5, O:0:3, D=3:3, s2; A=6:7, B=3:5, C=3:5, O=0:3, D=3:3	20
		160

APPENDIXES

Appendix 1. Cases, hypothetical distributions and results obtained by EA, PAE and 3ID for each of the 43 proposed hypotheses. Hypothetical distributions with the number of endemic species per area (spp) and the specific location of the cells occupied (x-y), where x is the row and y is the column.

CASE	HYPOTHETICAL DISTRIBUTIONS	RESULTS		
		EA	PAE	3ID
Non-conflictive patterns	1) 			
	2) 			
	3) 			
	4) 			
Overlapping patterns Type I	5) 			
	6) 			
	7) 			
	8) 			

CASE	HYPOTHETICAL DISTRIBUTIONS	RESULTS		
		EA	PAE	3ID
Overlapping patterns Type I	9) 			
Overlapping patterns Type II	10) 			
	11) 			
	12) 			
	13) 			
	14) 			
Overlapping patterns Type III	15) 			
	16) 			

CASE	HYPOTHETICAL DISTRIBUTIONS	RESULTS		
		EA	PAE	3ID
Overlapping patterns Type III	17) 			
	18) 			
	19) 			
	20) 			
Overlapping patterns Type IV	21) 			
	22) 			
	23) 			
	24) 			

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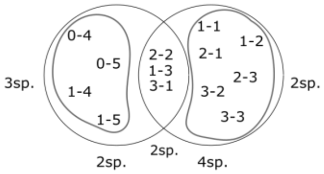
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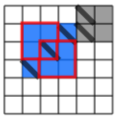
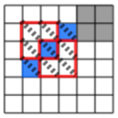
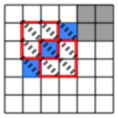
<td></td>
<td></td>
<td></td></tr>
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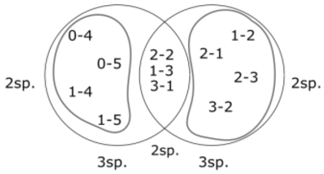
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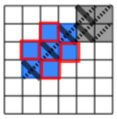
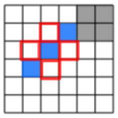
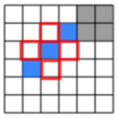
<td></td>
<td></td>
<td></td></tr>
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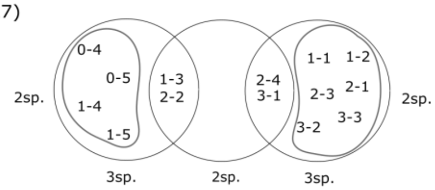
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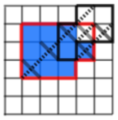
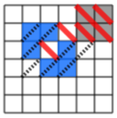
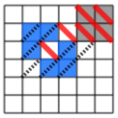
<td></td>
<td></td>
<td></td></tr>
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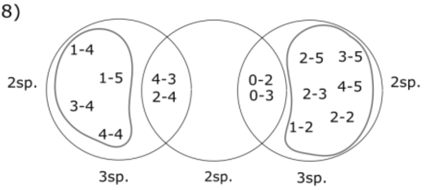
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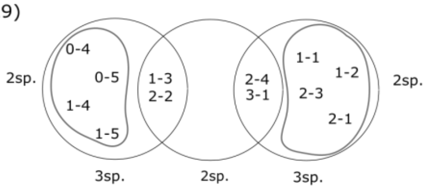
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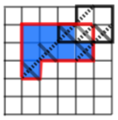
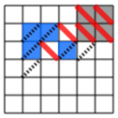
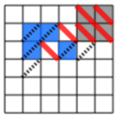
<td></td>
<td></td>
<td></td></tr>
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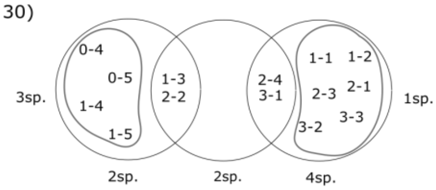
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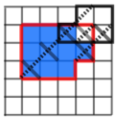
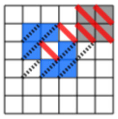
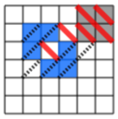
<td></td>
<td></td>
<td></td></tr>
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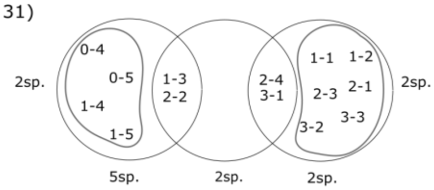
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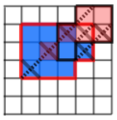
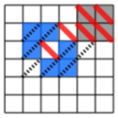
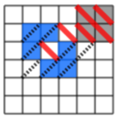
<td></td>
<td></td>
<td></td></tr>
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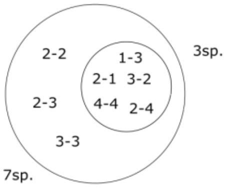
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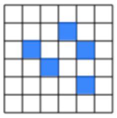
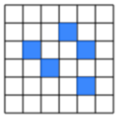
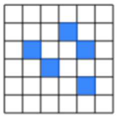
<td></td>
<td></td>
<td></td></tr>
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CASE	HYPOTHETICAL DISTRIBUTIONS	RESULTS		
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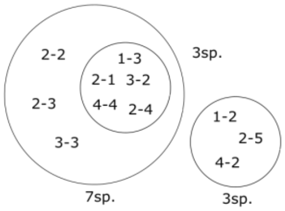
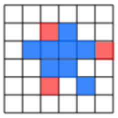
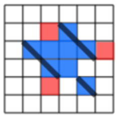
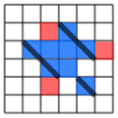
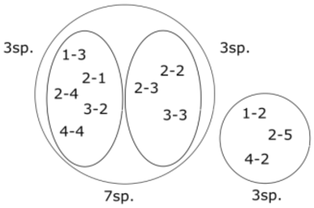
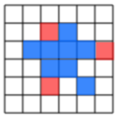
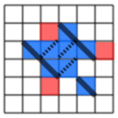
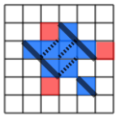
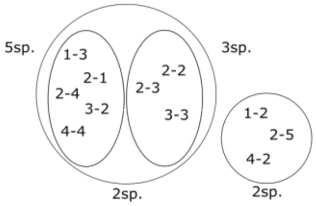
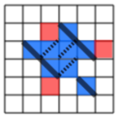
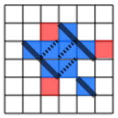
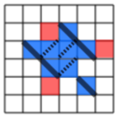
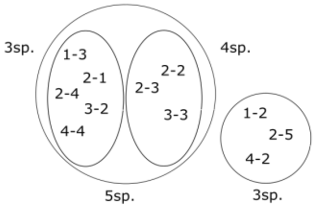
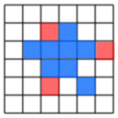
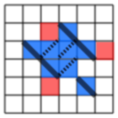
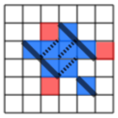
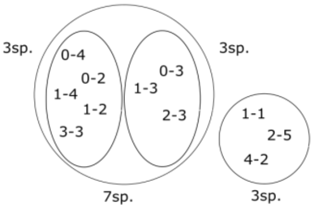
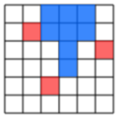
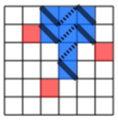
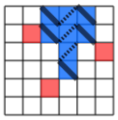
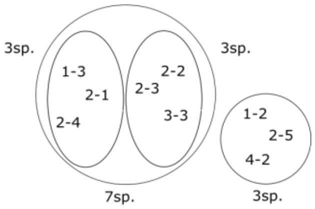
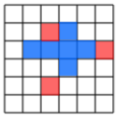
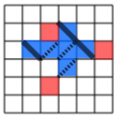
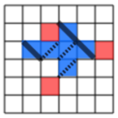
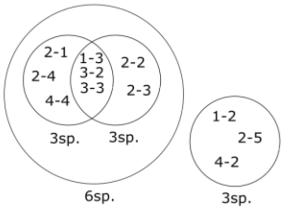
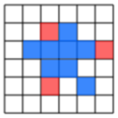
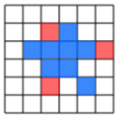
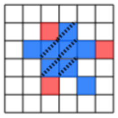
Nested patterns Type I	33) 			
	34) 			
	35) 			
	36) 			
	37) 			
	38) 			
Nested patterns Type II	39) 			

CASE	HYPOTHETICAL DISTRIBUTIONS	RESULTS		
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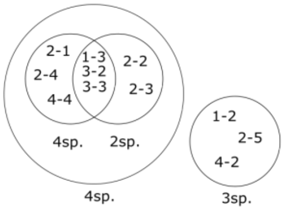
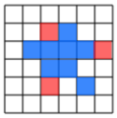
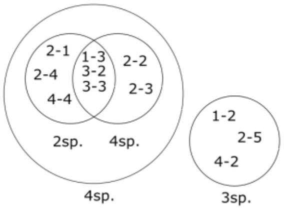
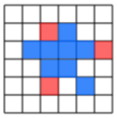
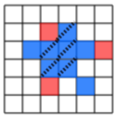
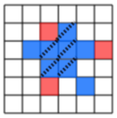
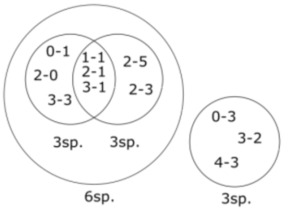
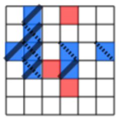
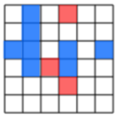
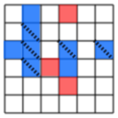
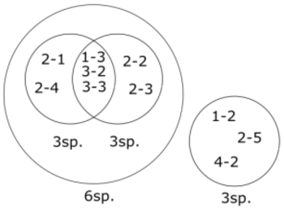
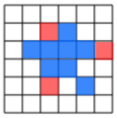
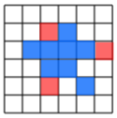
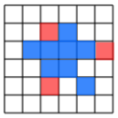
Nested patterns Type II	40) 			
	41) 			
	42) 			
	43) 			

Capítulo 3

Biogeographic patterns of benthic and planktonic hydrozoans from the southwestern Atlantic Ocean

Adriana Morales-Guerrero[1], Thaís P. Miranda[1], Carolina S. Rodriguez[2], Gabriel Nestor Genzano[2], and Antonio C. Marques[1,3]

[1]*Departamento de Zoologia, Universidade de São Paulo, R. Matão, Tr. 14, 101, 05508–090 São Paulo, SP, Brazil*

[2] *Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET-UNMdP, Mar del Plata, Argentina*

[3]*Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil.*

ABSTRACT

The rarity of studies on marine biogeographic patterns may be related to the lack of clear barriers in the oceanic system and to the three-dimensional capacity of occupation inherent to oceans. We analyzed patterns of distribution of benthic, pelagic and benthopelagic non-siphonophore hydrozoans of the southwestern Atlantic Ocean (SWAO) to test previous hypotheses of regionalization and to propose additional hypotheses of biotic elements for the SWAO. Distribution data for 214 hydrozoan species from the SWAO (20°-60°S, 33°-75°W) were organized in different data matrices (Concatenated, Benthic, Pelagic, and Benthopelagic) according to the different life-cycle strategies in Hydrozoa. All matrices were analyzed using the Endemicity Analysis (EA), Three-Item Analysis of Distributions (3ID), and Parsimony Analysis of Endemism (PAE). The resulting areas showed three broad patterns, (1) Tropical, (2) Warm-Temperate and (3) Cold-Temperate, all of which concord with previous biogeographic hypotheses for the SWAO. The output patterns varied according to the life cycle, demonstrating the importance of separate analyses for different life-cycle strategies. Each method performed differently, and we concluded that the use of 3ID and EA as complementary methods is the best approach to provide inferences on marine biogeographic patterns.

RESUMO

A escassez de estudos sobre padrões biogeográficos marinhos pode estar relacionada com a falta de barreiras geográficas claras no sistema oceânico e à capacidade tridimensional de ocupação inerente aos oceanos. Neste estudo, foram analisados os padrões de distribuição geográfica de 214 espécies de hidrozoários bentônicos, pelágicos e bentopelágicos não sifonóforos do Oceano Atlântico Sul Ocidental (OASO; 20°-60°S, 33°-75°W), para testar hipóteses anteriores de regionalização biogeográfica e propor novas abordagens nesse contexto. Os dados foram organizados em diferentes matrizes (concatenada, bentônica, pelágica, e bentopelágica) de acordo com as diferentes estratégias do ciclo de vida em Hydrozoa. Todas as matrizes foram analisadas por meio da Análise de Parcimônia de endemicidade (PAE), da Análise de Endemicidade (EA) e a Análise de Distribuições de Três-Itens (3ID). Os resultados mostram três padrões gerais: (1) Tropical (2) Temperado-Quente, e (3) Temperado-Frio, todos concordantes com hipóteses biogeográficas anteriores para a região. Os padrões obtidos variam de acordo com o tipo de ciclo de vida em Hydrozoa, demonstrando a importância de analisar-se separadamente conjuntos de dados de espécies com diferentes estratégias de reprodução. Cada método teve um desempenho diferente e nós concluímos que o uso de 3ID e EA em conjunto é a melhor opção para fornecer inferências sólidas sobre padrões biogeográficos marinhos.

Key words: marine realm, Endemicity Analysis, Three-Item Analysis of Distributions, Parsimony Analysis of Endemicity, Tropical, Warm-region, Cold-region, Biogeography

INTRODUCTION

The Medusozoa is an ancient taxon with simple morphology but with a high richness of life cycles (Marques & Collins, 2004; Collins *et al.,* 2006; Van Iten *et al.,* 2006, 2014; Cartwright *et al.,* 2008). The Hydrozoa is the most speciose taxon of Medusozoa, with ca. 3,800 species, although the taxonomic status of many of them is unclear (Schuchert 2015). Their most remarkable biological feature may be the metagenic life cycle, in which polyp, medusa and medusoid stages may be present; although many degrees of reduction, or even suppression, also occur (e.g., Leclère *et al.,* 2009; Cartwright & Nawrocki, 2010; Maronna *et al.,* 2015; Mendoza-Becerríl *et al.,* submitted). These complex life cycles make hydrozoans an interesting and useful group to study regionalization patterns, mainly because their current distribution results from benthic and pelagic processes, sometimes with different ecophysiological and distributional requirements (Mendoza-Becerríl *et al.*, 2013). Also, metagenic life cycles may allow one to study dispersal abilities in the three-dimensional marine environment (Marques & Peña Cantero, 2010).

Continental or marine regional patterns with non-random distributional congruence among taxa have several different denominations (Morrone, 2014), such as areas of endemism, biotic components, biotic elements or biotic assemblages (Salthe, 1985; Cracraft, 1994; Morrone, 1994, 2014; Hausdorf, 2002). The formation of a biotic element may derive from many ecological or historical processes (Platnick, 1991; Harold & Mooi, 1994; Linder, 2001; Morrone, 2014; Szumik & Goloboff, 2004). Therefore, concepts of biotic elements cannot be limited to any specific causal factor. Additionally, and perhaps somewhat contradictorily, several alternatives can be used to determine biotic elements, including null models (Mast & Nyffeler, 2003; Giokas & Sfenthourakis, 2008), algorithms from phylogenetics (e.g. Parsimony Analysis of Endemicity, PAE, Morrone, 1994; Cladistic Analysis of Distributions and Endemism, CADE, Porzecanski & Cracraft, 2005; García-Barros *et al*., 2002; Nested Areas of Endemism Analysis, AoE, Deo & DeSalle, 2006; Three-Item Analysis of Distributions, 3ID, Nelson & Platnick, 1991; Morales-Guerrero *et al*., 2015), optimality criteria explicitly developed for evaluating candidate biotic elements (Endemicity Analysis, EA, Szumik *et al*., 2002; Szumik & Goloboff, 2004), among others. PAE is the method most often used in empirical analyses (Casagranda *et al.*, 2012), followed by EA (e.g. Aagesen, *et al.*, 2009; Navarro, *et al.*, 2009; Szumik *et al.*, 2012; Prado *et al.*, 2014; Martínez-Hernández *et al.*, 2015; Noguera-Urbano & Escalante, 2015). A recent comparison among PAE, EA and 3ID, using hypothetical distributions, concluded that 3ID together with EA is the best methodological option to infer nested biotic elements and overlapping distributions (Morales-Guerrero *et al.*, 2015).

Studies on marine biotic elements and on marine biogeographic patterns are few, compared with the corresponding number of studies for the terrestrial realm (Miranda & Marques, 2011; Miranda *et al*., 2013). This may be related to the apparent lack of clear barriers in the oceanic system, and to the three-dimensional capacity for occupation inherent to the habitat (Miranda & Marques, 2011; Bowen *et al*., 2013). These difficulties have resulted in a division of the discipline of marine biogeography into benthic (shallow or deep-sea) and pelagic (coastal or oceanic) studies (cf. Okolodkov, 2010). A few marine biogeographic studies have been conducted for crustaceans, polychaetes, cnidarians, etc. (De Grave, 2001; Santini, 2002; Moreno *et al*., 2006; Winfield *et al*., 2006; Floeter *et al*., 2008; Marques & Peña Cantero, 2010; Miranda *et al*., 2013, 2015), and a few others have dealt with analyses of parametric biogeography of coral-reef fishes and squat lobsters (e.g. Cabezas *et al.*, 2012; Cowman & Bellwood, 2013).

During the second half of the 20th century, marine biogeographers defined large biotic elements encompassing smaller provinces (Ekman, 1953; Briggs, 1974; Vermeij, 1978). This regionalization was based on endemic taxa, mainly fishes, from continental shelves, abyssal depths, and open oceanic areas. Subsequently, other approaches, databases, and criteria have been used to improve these inferences. For the southwestern Atlantic Ocean (SWAO), four biogeographic regions are distinguished: Antarctic, Cold-Temperate, Warm-Temperate, and Tropical (Briggs, 1995; Bailey, 1998; Briggs & Bowen, 2012, 2013; Servais *et al.*, 2013). Spalding *et al.* (2007) divided its southern part into two provinces (Warm Temperate Southwestern Atlantic and Magellanic) and nine ecoregions: Southeastern Brazil, Rio Grande, Rio de la Plata, Uruguay-Buenos Aires Shelf, North Patagonian Gulfs, Patagonian Shelf, Malvinas/Falklands, Channels and Fjords of Southern Chile and Chiloense (Fig. 1). More recently, in a review of the classification of the pelagic oceanic waters of the world, Spalding *et al.* (2012) proposed two pelagic provinces for the SWAO: South Central Atlantic and Falkland/Malvinas Current.

Biogeographic studies in the SWAO are few (Briggs, 1974; Vermeij, 1978; Palacio, 1982; Genzano *et al.*, 2009). A recent study was based on EA and on the distribution of 130 species of benthic hydroids in the region between 22° and 55°S, in which three main biotic elements were defined for the SWAO: Tropical, Subtropical, and disjunctions along these two patterns (Miranda *et al.*, 2015). Other biogeographic studies using benthic hydroid distributions in the Atlantic Ocean (AO) and adjacencies are those of Medel & López-González (1998), Gibbons *et al.* (2010a), Marques & Peña Cantero (2010) and Miranda *et al.* (2013). Based on different life-cycle strategies in Hydrozoa, Gibbons *et al.* (2010) demonstrated that holoplanktonic species have less biogeographic structure than meroplanktonic species, which in turn have less biogeographic structure than benthic species (Gibbons *et al.*, 2010a). Approaches such as this are uncommon when dealing with geographic distribution patterns of hydrozoans, and comprise an interesting line of study that might help to clarify the biogeographic history of diversification of the taxon. Accordingly, we analyzed the patterns of distribution of benthic, pelagic and benthopelagic non-siphonophore hydrozoans of the SWAO, using PAE, EA and 3ID to test previous hypotheses of regionalization (*viz.* Spalding *et al.*, 2007, 2012; Briggs & Bowen, 2012, 2013; Miranda *et al.*, 2015), and to propose additional biogeographic hypotheses for biotic elements in the SWAO.

MATERIAL AND METHODS

Study region and data sources.— We studied the southwestern Atlantic Ocean including coastal and neritic waters between 20°-60°S and 75°-33°W (Fig. 2). We compiled a database of 214 hydrozoan species, including the three main types of life-cycle strategies in the class (Appendix 1). Data for benthic hydrozoans were from primary data (Miranda *et al.*, 2015), and the database was completed with primary data for planktonic species. We reviewed and checked all the biogeographic records. Some taxa are endemic to the study region (*Aglauropsis kawari, Corymorpha januarii, Ectopleura obypa, Eudendrium caraiuru, Hydractinia uniformis, Lytocarpia canepa, Olindias sambaquiensis, Parascyphus repens, Plumularia insignis, Ralpharia sanctisebastiani, Symplectoscyphus magellanicus*), and others have also been recorded elsewhere. We divided the database into subsets of "Benthic" (93 species), "Pelagic" (46 species) and "Benthopelagic" (75 species), according to their life cycles, and also concatenated the three subsets into a single combined dataset for a universal analysis. Benthic hydrozoans with a medusoid stage were included in the benthopelagic analyses. Based on the qualitative combined criteria C2 and C3 for delimitation of areas of endemism recently proposed by DaSilva *et al.* (2015), we relaxed the concept of endemism by considering a biotic element as a set of one or more taxa restricted to a geographic area but not exclusive to it (i.e., we also used geographic information for widespread species; see similar examples in Oliveira *et al.*, 2015; Miranda *et al.*, 2015). This is in accordance with the wide patterns of geographic distribution of most hydrozoan species, suggesting a wide variety of potentially contrasting biogeographic hypotheses, which increases the accuracy of the dataset analyzed (Miranda *et al.*, 2015).

Biogeographic analyses.— All datasets (Benthic, Pelagic, Benthopelagic, and Concatenated) were analyzed according to different biogeographic methods for inference of biotic elements. We used three different grid-cell sizes (2x2°, 3x3° and 4x4°), all of them with the same latitudinal and longitudinal origin (see Aagesen *et al.*, 2009; Escalante *et al.*, 2010, 2013), in order to recover the scale with the most accurate biogeographic pattern, i.e., without generation of disjunctive and/or overlapping areas.

The first biogeographic method was the EA (Szumik *et al.*, 2002; Szumik and Goloboff, 2004), based on the heuristic algorithm of NDM-VNDM version 3.0 (Goloboff, 2011). We ran the analyses using the default parameters; cells were swapped one cell at a time, with the search repeated 100 times, and those sets with one or more species were saved as biotic elements. The results were synthesized by the consensus option of NDM-VNDM (Aagesen et al., 2013), where all biotic elements that shared 50% of the taxa with at least one other area were saved.

The second method was the 3ID (Nelson & Platnick, 1991; Morales-Guerrero *et al.*, 2015), based on a phylogenetic analysis of a three-statement matrix derived from the original distribution dataset. The three-statement matrix was generated using TAXODIUM 1.0 (Mavrodiev & Madorsky, 2012), using their fractional weights (Nelson & Ladiges, 1992). The phylogenetic analysis was performed in the software TNT (Goloboff *et al.*, 2008), using a heuristic search generating 100 Wagner trees with random addition sequences (mult/100) and keeping 10 cladograms in memory for each of them (Hold/10). The strict consensus was applied to summarize all results.

The third method was PAE, which was based on a phylogenetic analysis of binary distributions and heuristic search, under the same criteria used in 3ID.

RESULTS

All the methods resulted in disjunctive areas when the Concatenated matrix was analyzed by using grids of 2X2°. In contrast, the 4X4° grid resulted in overlapping biogeographic patterns. Finally, the 3X3° grid resulted in consistent patterns (Table 1), and for this reason it was adopted as our working analysis. Lists of the species determining each biotic element are provided for each method (Appendixes 2-4).

Concatenated Analysis.— The EA resulted in 98 biotic elements (Fig. 3A). Three general patterns appeared (Table 2): (1) Tropical (T1), (2) Warm-Temperate (T2) and (3) Cold-Temperate (T3) (Fig. 3A), supported by different numbers and compositions of species. 3ID resulted in four biotic elements (Fig. 3B): (1) Warm region (T4) with two major nested clades (Fig. 3B, shades of green); (2) Cold-Temperate region along 47–56°S (Fig. 3B, blue); (3) and (4) two independent biotic elements in the Falkland/Malvinas Current (Fig. 3B, gray and yellow, T5-6). The PAE resulted in four biotic elements (Fig. 3C): (1) Tropical region (Fig. 3C, light green);

(2) Rio Grande province (Fig. 3C, red, T7); (3) Uruguay-Buenos Aires Shelf (Fig. 3C, dark green, T8); (4) Cold-Temperate oceans on the Patagonian Shelf (Fig. 3C, blue).

Benthic analysis.— The EA resulted in 19 biotic elements (Fig. 4), with two general patterns (Table 2): (1) Tropical (B1), with 10 biotic elements, supported by 6-26 species (Fig. 4A, green); and (2) Warm-Temperate (B2), with three biotic elements, supported by 5-7 species along 36–45°S (Fig. 4A, purple). The hierarchical methods (3ID and PAE) resulted in three general patterns: (1) Tropical, (2) Warm-Temperate, and (3) a more-offshore group in the Falkland/Malvinas Current (B3), supported by *Tulpa tulipifera* (Fig. 4B-C).

Pelagic analysis.— The EA resulted in nine biotic elements (Table 2), with two general patterns (Fig. 5): (1) Warm region (P1), along 25–41°S, including seven biotic elements supported by 4-8 species (Fig. 5A, orange); and (2) Cold-Temperate region (P2), with two biotic elements supported by 4-5 species (Fig. 5A, blue). The 3ID resulted in two general patterns similar to those of EA (Fig. 5B, orange and blue), and another group in the Falkland/Malvinas Current (P3) supported by *Cunina duplicata* (Fig. 5B, gray). The PAE resulted in only one small biotic element, in the middle of the Tropical and Warm-Temperate regions along 25–35°S (Fig. 5C).

Benthopelagic analysis.— The EA resulted in 31 biotic elements (Fig. 6), organized in three general patterns (Table 2): (1) Tropical (BP1), with the highest endemicity scores (2.25-7.00) and the largest number of species (5-10 species); (2) Warm region (BP2), with scores of 2.01-4.29 (Fig. 6A (*) – green+purple) and 4-6 species. In this case the Warm-Temperate region (single purple region in Fig. 6A) received lower scores (2.05-3.48) than the warm region; and (3) Cold-Temperate (BP3), a small biotic element along 52–56°S (Fig. 6A, blue). 3ID resulted in 2 biotic elements (Fig. 6B): (1) Warm region (Fig. 10, green), in which two major clades were nested (Fig. 6B, shades of green); and (2) A small Cold-temperate biotic element on the Patagonian Shelf (Fig. 10, blue). The PAE did not result in any solution with clades supported by unequivocal synapomorphies in this case.

DISCUSSION

Southwestern Atlantic Ocean patterns.— Our results revealed three major patterns in the SWAO, (1) Tropical, (2) Warm-Temperate, and (3) Cold-Temperate, all of them congruent with previously proposed biogeographic schemes (Briggs & Bowen 2012, Spalding *et al.*, 2007). These patterns are associated with abiotic conditions (*e.g.*, temperature, salinity, nutrient concentrations) and oceanic fronts of the southwestern Atlantic Ocean. The Tropical region is part of the Brazilian Province (Briggs & Bowen, 2012), extending from the mouth of the Amazon River to the state of Santa Catarina in southern Brazil (Floeter *et al.*, 2008). In the classification of Spalding et al. (2007), this region corresponds to the Southeastern Brazil ecoregion, between the Cape Frio upwelling (22°S) and Cape Santa Marta Grande (32°S). About 25% of the coral and fish species of the Tropical region are endemic (Veron, 2000; Briggs & Bowen, 2012), and ocean circulation is dominated by the warm Brazil Current. The present oceanographic dynamics derived from winds, tides, freshwater discharges, and oceanic currents might be hypothesized as a barrier to species distributions (Acha *et al*., 2004).

The Warm-Temperate region extends from Santa Catarina state (Brazil) to the Valdez Peninsula (Argentina), and includes the Rio Grande, Uruguay-Buenos Aires Shelf, Rio de la Plata, and North Patagonian Gulf ecoregions (cf. Spalding *et al.,* 2007). This region is distinguished by its high endemism, and is separated from tropical waters by temperature differences of 20°C in the coldest month (Briggs, 1974). Temperature acts as a barrier preventing the dispersal of many tropical species. Relict and constrained fauna may be also related to barriers in the region, such as its three large estuarine fronts (Patos Lagoon, Río de la Plata and El Rincón) and the tidal front at the Valdez Peninsula (Acha *et al*., 2004). Oceanic circulation is dominated by the opposing Brazil (tropical/subtropical) and Falkland/Malvinas (subantarctic) currents, making the Warm-Temperate region an area of high biological production (Acha *et al*., 2004).

The Tropical and Warm-Temperate regions were also found in two other biogeographic analyses based on benthic hydroids from the Atlantic. In the first study they were named the Brazilian Subregion and Bonaerensian Province, respectively, and were shown to have high endemism (Medel & López-González, 1998). In the second study, these areas were named Tropical and Subtropical areas, respectively, and were accompanied by hypotheses of independence and disjunction (Miranda *et al.*, 2015).

The Cold-Temperate region around southernmost South America and the Falkland/Malvinas Islands corresponds to the Southern Argentina province and Magellanic ecoregion (Spalding *et al.,* 2007; Briggs & Bowen, 2012). Fewer species are restricted to the Cold-Temperate region than in other regions, probably because Cold-Temperate biotas were ultimately derived from Tropical species that became adapted to this new habitat (Krug *et al.*, 2009). A similar pattern occurs at supraspecific levels, in which many families and genera occur widely in the Tropical and Warm-Temperate regions, but relatively few inhabit the Cold-Temperate region (Briggs, 1995; Grant *et al.,* 2010). The Cold-Temperate region is a unique habitat characterized by extreme physiological demands. Temperatures (2-12°C in the coldest month), low salinity, and oceanic circulation dominated by the Falkland/Malvinas Current function as ecological barriers, resulting in higher rates of endemism for invertebrates (Griffiths *et al.*, 2009).

Two ‘extra’ minor biotic elements, not previously reported, occur near the Argentinean shelf-break (Figs. 3B, 4A-B, 5B, yellow and gray). Subantarctic shelf waters of the region merge with cold saline waters of the Falkland/Malvinas Current (Fig. 7), resulting in a thermohaline front (Martos & Piccolo, 1988; Lutz & Carreto, 1991). The shelf-break front is a permanent feature on the border of the shelf, but the exact geographic location of the front varies according to the dynamics of the Falkland/Malvinas Current (Acha *et al.,* 2004). The opposing flows of subantarctic waters and the Falkland/Malvinas Current probably drive hydrozoan speciation in these two biotic elements.

Life cycles influencing distribution.— The different life cycles resulted in different patterns. The seasonality and population dynamics of hydrozoan species (Gili & Hughes, 1995; Migotto *et al.,* 2001; Bavestrello *et al.,* 2006; Rossi *et al.*, 2012; Fernandez *et al.,* 2014, 2015) are influenced by marine abiotic and biotic factors that, ultimately, may constitute geographic barriers for species with certain life-cycle strategies (Miranda *et al.*, 2015).

The Concatenated analysis revealed six patterns (T1-T6, Table 2), and the Benthic analysis revealed three (B1-B3, Table 2), missing the Cold-Temperate pattern, perhaps due to a sampling effect. The quality of outputs in biogeographic methods depends on the total number of species analyzed, and the Cold-Temperate region included only 6 benthic species (6.45% of a total of 93 spp.: *Lafoea dumosa, Symplectoscyphus subdichotomus, Sertularella mediterranea, Plumularia strictocarpa, Plumularia setacea,* and *Halecium delicatulum*). Similar patterns between the Concatenated and Benthic analyses are related to shared species of their data matrices: 37 and 9 shared benthic species, of the totals of 56 and 27 species for the Tropical and Warm-Temperate regions, respectively.

Most Warm-Temperate provinces are presumed to be related to the neighboring Tropical province, because of their phylogenetic and taxonomic affinities (Briggs & Bowen, 2012).

Therefore, one could expect the provinces to be divided into *warm* (Temperate and Tropical) and *cold* (Temperate and Cold) groups. The Pelagic analysis resulted in three patterns, including a large *warm group* (P1-P3, Figs. 7-8). Pelagic hydrozoan populations inhabit a dynamic and dispersive, although structured, fluid medium (Acha *et al.,* 2004). Classically, the medusa stage is considered the main mechanism for successful dispersal in hydrozoans, almost invariably traveling long distances before the planula release, and any advantage of a close association is lost (Gibbons *et al.,* 2010b). There would be a relationship among richness, distribution and life-cycle strategy for Hydrozoa, and life-cycle data would support the assumption that pelagic taxa have a greater dispersal capacity and less biogeographic structure than the other life stages (Gibbons *et al.,* 2010a, b). Indeed, the present pelagic analysis revealed hydrozoans with a higher dispersive capacity, crossing putative barriers that could be expected for other types of life cycles, such as benthic. This capacity result in sister taxa with adjacent (parapatric), overlapping, or even identical (sympatric) distributions (Bowen *et al.,* 2013). Intermittent historical barriers that could generate speciation between the Warm-Temperate and Tropical regions might have been ineffective in view of the high dispersal capacity of the medusa, and this could explain why this pattern was not recovered by the Pelagic analysis, but the Cold-Temperate region still had a strong barrier. Likewise, similar patterns between the Concatenated and Pelagic analyses are related to the shared species of these data matrices (13 and 6 shared Pelagic species of the total of 43 and 11 species for the Warm and Cold-Temperate regions, respectively).

The Benthopelagic analyses resulted in three patterns (BP1-BP3). Differently from Cornelius' hypotheses (1991, 1992), this analysis suggested that meroplanktonic species have a less biogeographic structure than benthic species, crossing barriers between the Tropical and Warm-temperate regions. This is probably related to the interaction between oceanographic conditions and dispersal capacity (Gibbons *et al.,* 2010b), even though the barrier between the Warm and Cold-Temperate remains strong. This analysis did not retrieve the two minor biotic elements of the Argentinean shelf-break, perhaps because of insufficient sampling. Similar patterns between the Concatenated and Benthopelagic analyses are, again, related to shared species of the matrices (15 and 19 benthopelagic species of the totals of 56 and 43 species, for the Tropical and Warm regions, respectively).

Our data support the hypothesis that, for hydrozoans, the delimitation of biotic elements in marine habitats varies according to the different life-cycle strategies, as may occur in the biogeography of any other taxa with complex life cycles. Biogeographic patterns are influenced by the life history of the species, regardless of whether these similar life histories are phylogenetically or functionally determined. Taxa without dispersal stages in their life history would be more influenced by climatic and tectonic events. Contrastingly, the biogeography of widely distributed pelagic or benthopelagic taxa reflects local oceanographic conditions, but their speciation would be limited by their dispersal ability (Gibbons *et al.,* 2010b).

Performance of the Methods.— The 3ID method retrieved a hypothetical division into warm and cold regions (Briggs & Bowen, 2012): a Warm region with two nested patterns (Tropical and Warm-Temperate regions, Figs. 4b, 6b), and the two biotic elements near the Argentinean shelf-break front (Figs. 4, 6, 8, yellow and gray). The EA results showed higher endemicity scores for the Warm region than for the Tropical and Warm-Temperate regions (Fig. 6) only in the Benthopelagic analysis, and therefore the division of the Warm region is uncommon in most cases. The PAE results never recovered the warm and cold split, but most analyses recovered either the Tropical/Warm-Temperate division, or one of these regions, or even none (Fig. 5c). PAE recovered one biotic element near the Argentinean shelf-break front, but only in the Benthic analysis (Fig. 6, yellow).

Thus, the PAE proved to be less efficient than the 3ID and EA. The PAE obtained fewer biotic elements (e.g., for the Pelagic analysis) and inconsistent patterns compared to traditional biogeographic hypotheses (e.g., for the Concatenated analysis); and failed to find distribution patterns (e.g., for the Benthopelagic analysis). On the other hand, the 3ID and EA proved to be consistent methods for biogeographic inferences, as previously suggested by Morales-Guerrero *et al.* (2015). Therefore, based on our results, we recommend the use of the 3ID and EA as complementary methods to infer diversification patterns for marine biotas.

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FIGURES AND TABLES

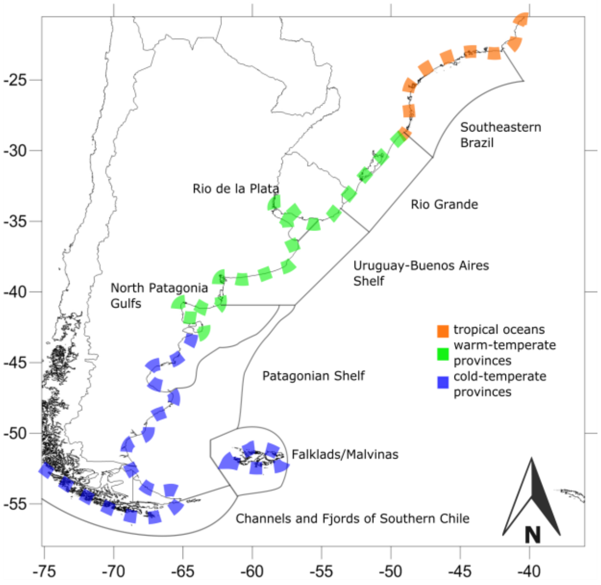

Figure 1. Biogeographic areas and ecoregions of the southwestern Atlantic Ocean. Orange, green and blue define biogeographic areas, black lines border ecoregions (modified from Briggs and Bowen 2012, Spalding *et al.*, 2007).

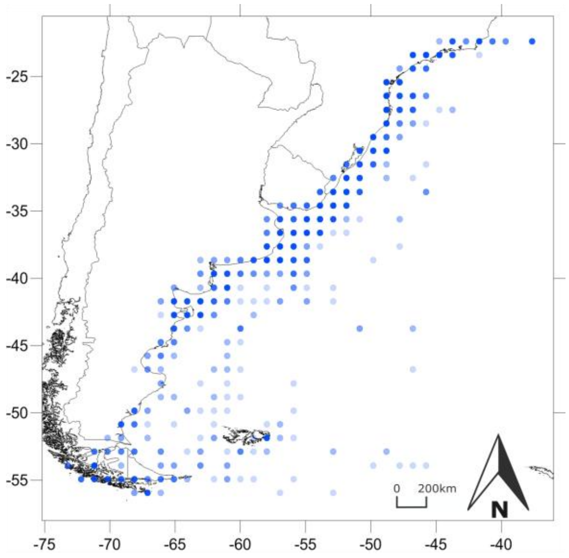

Figure 2. Study region in the southwestern Atlantic Ocean for the 214 hydrozoan species. Points indicate the sampling sites. Dark points indicate higher species richness than light ones.

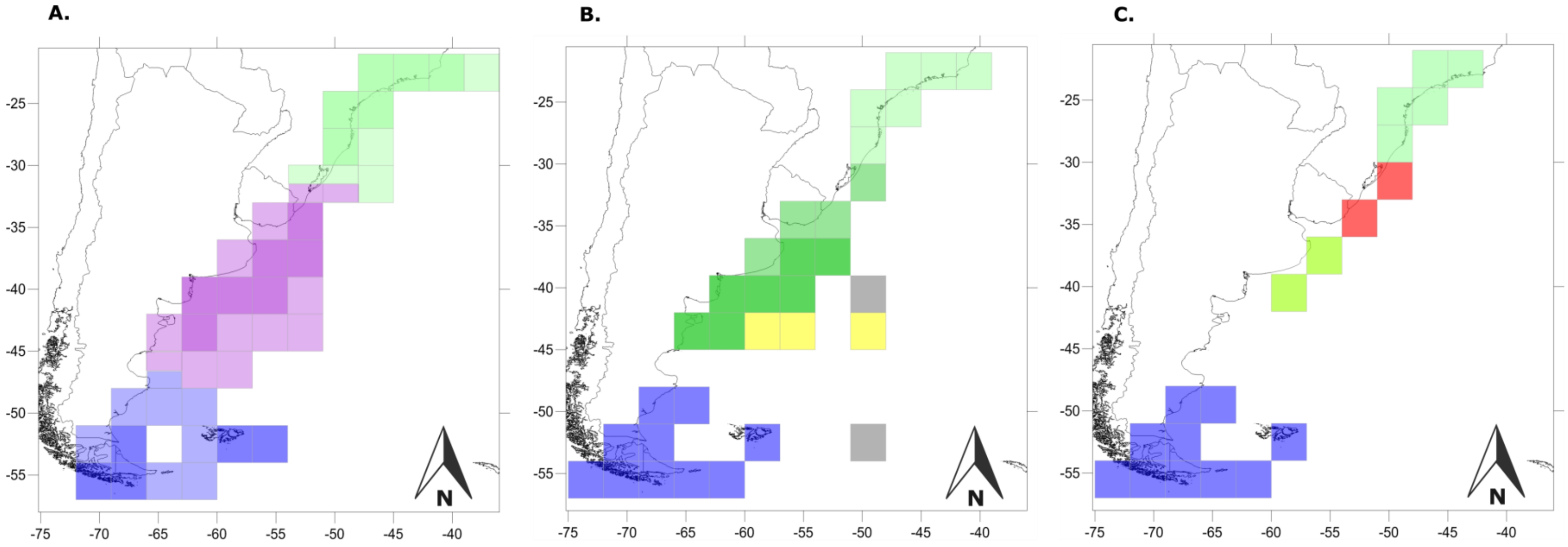

Figure 3. Patterns for Concatenated data matrix (214 hydrozoan species). (A) Endemicity analysis (EA), (B) Three-item analysis of distributions (3ID), (C) Parsimony Analysis of Endemicity (PAE). Darker cells indicate higher endemism scores for EA or nested biotic elements for 3ID. Biotic elements are illustrated on a grid of 3X3°. For EA the patterns are summarized as follows, green region: 20 biotic elements, 7-36 species in the area (spp.), Endemicity Scores (ES) = 4.11-**28.7**; purple: 17 biotic elements, 3-14 spp., ES = 2.33-**8.70**; blue: 4 biotic elements, 6-7 spp., 3.19-**4.49**. 57 patterns are related to other groups of areas with low endemism scores: green+purple: 44 biotic elements, 3-13 spp., ES = 2.15-8.48; purple+blue: 4 biotic elements, 3-5 spp., ES = 2.45-3.47; green+purple+blue: 9 biotic elements, 3-7 spp., ES = 2.12-3.95.

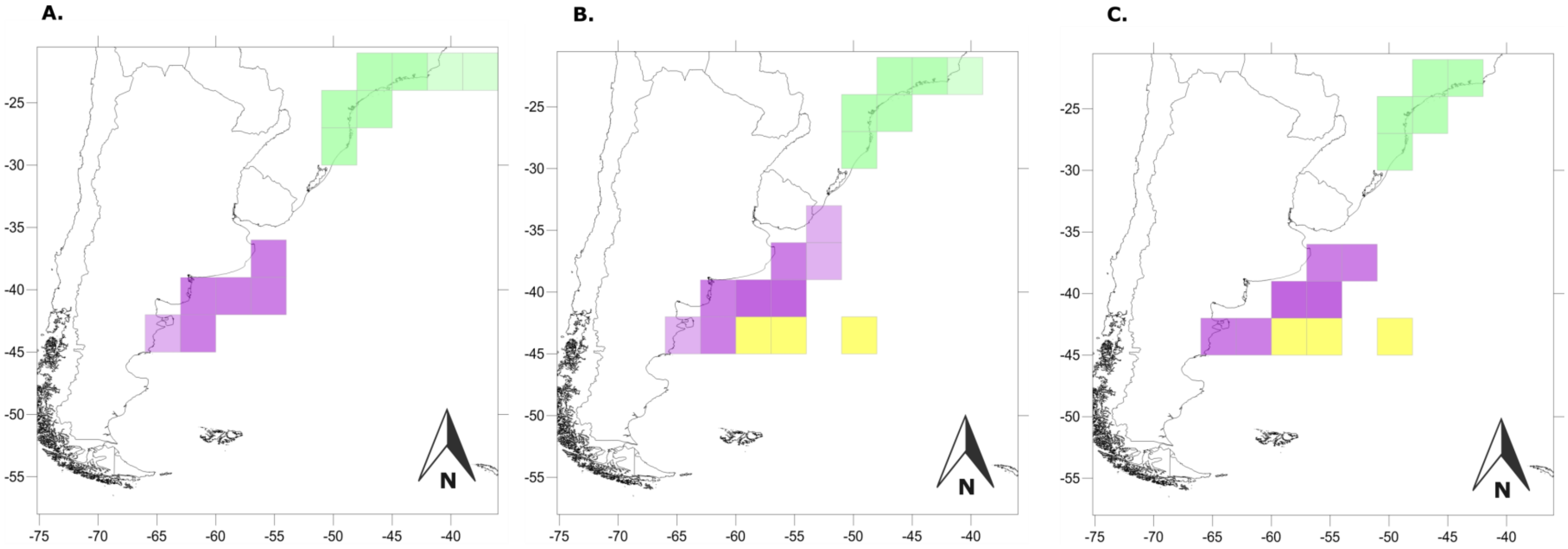

Figure 4. Patterns for Benthic data matrix (93 species of Hydrozoa). (A) Endemicity analysis (EA), (B) Three-item analysis of distributions (3ID), (C) Parsimony Analysis of Endemicity (PAE). Darker cells indicate higher endemism scores for EA or nested biotic elements for 3ID. Biotic elements are illustrated on a grid of 3X3°. For EA the patterns are summarized as follows: green region: 11 biotic elements, 6-27 spp., Endemicity Scores (ES) = 2.02-**20.26**; and purple: 3 biotic elements, 5-7 spp., ES = 2.83-**4.22**. 5 patterns are related to these groups of areas with low endemism scores: green+purple: 5 biotic elements, 5-6 spp., ES = 3.27-3.38.

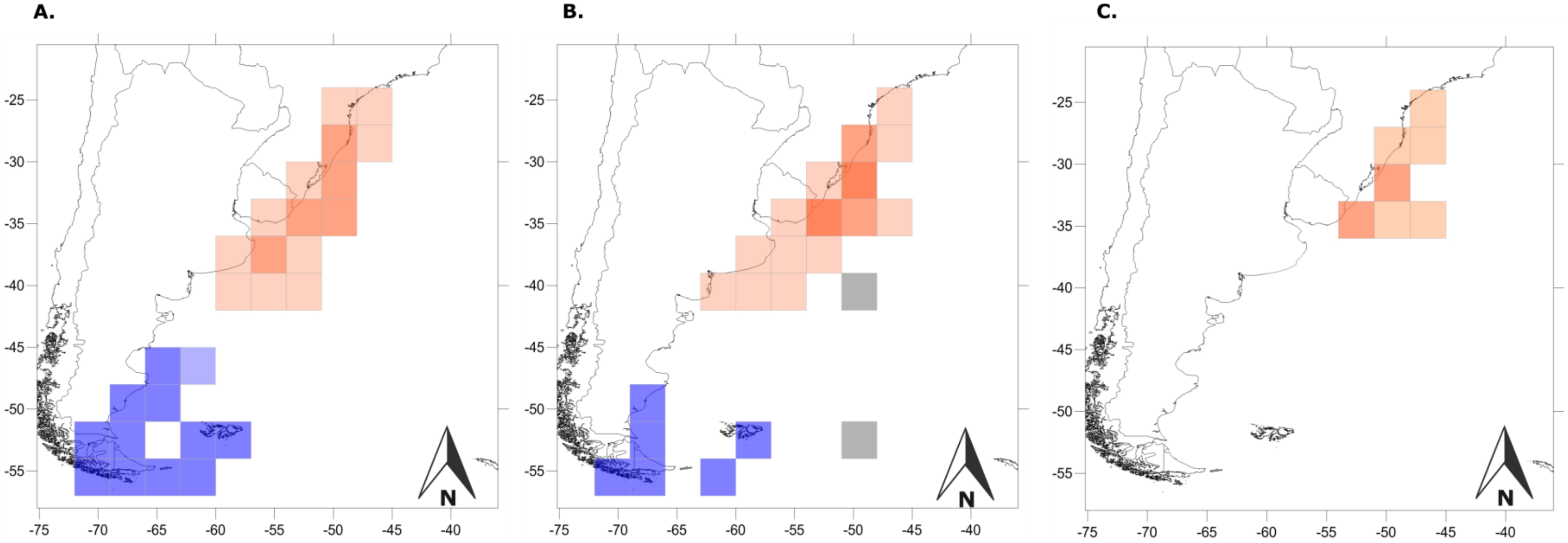

Figure 5. Patterns for Pelagic data matrix (46 species of Hydrozoa). (A) Endemicity analysis (EA), (B) Three-item analysis of distributions (3ID), (C) Parsimony Analysis of Endemicity (PAE). Darker cells indicate higher endemism scores for EA or nested biotic elements for 3ID. Biotic elements are illustrated on a grid of 3X3°. For EA the patterns are summarized as follows: orange region: 7 biotic elements, 4-8 spp., Endemicity Scores (ES) = 2.00-**5.37**; and blue: 2 biotic elements, 4-5 spp., ES = 3.39-**3.59**.

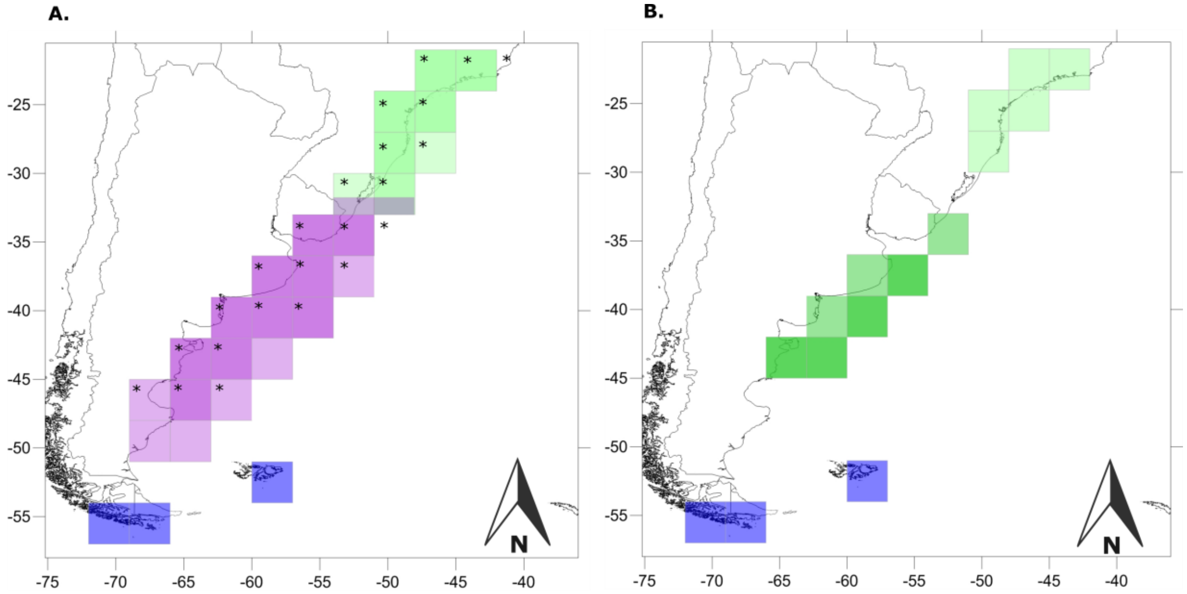

Figure 6. Patterns for Benthopelagic data matrix (75 species of Hydrozoa). (A) Endemicity analysis (EA), (B) Three-item analysis of distributions (3ID). Darker cells indicate higher endemism scores for EA or nested biotic elements for 3ID. Biotic elements are illustrated on a grid of 3X3°. For EA the patterns are summarized as follows: green region: 4 biotic elements, 5-10 spp., Endemicity Scores (ES) = 2.25-**7.00**; purple: 7 biotic elements, 3-7 spp., ES = 2.05-3.48; blue: 1 biotic element, 2 spp., ES = **2.00**. Some patterns are related to these groups (*): green+purple: 19 biotic elements, 4-6 spp., ES = 2.01-**4.29**.

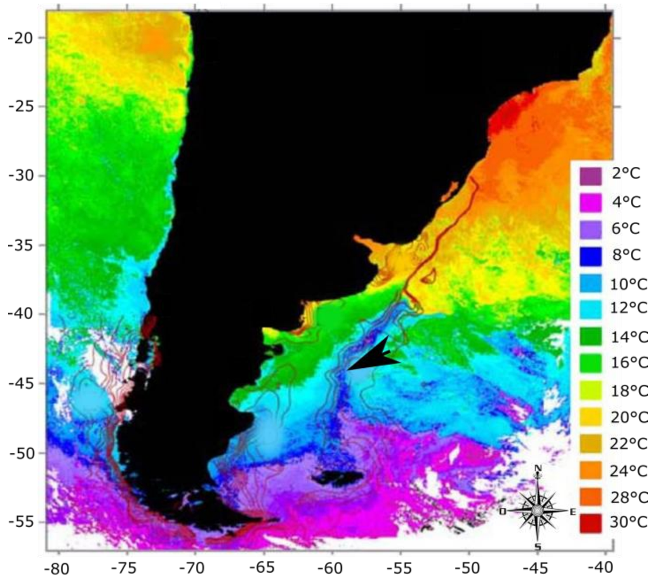

Figure 7. Temperature of sea-surface waters over southern South Atlantic continental shelf. Black arrow: Argentinean shelf-break front. Modified from Acha *et al.*, 2004.

Table 1. Grid cell size with number of solutions obtained by Endemicity Analysis (EA) and its consensus (EA cons.), Three-Item Analysis of Distributions (3ID), and Parsimony Analysis of Endemicity (PAE) for the distribution of 214 species of Hydrozoa.

Grid cell size	Number of solutions for method			
	EA	EA Cons.	3ID	PAE
2°X2°	49	13	6	3
3°X3°	98	15	4	4
4°X4°	152	15	3	3

Table 2. Number of biotic elements and respective general patterns resulting from Endemicity Analysis (EA), Three-Item Analysis of Distributions (3ID), and Parsimony Analysis of Endemicity (PAE) for each database constructed. Be: Biotic elements found by each method.

Analysis	EA	General patterns	3ID	General patterns	PAE	General patterns
Concatenated analysis	98 Be	Tropical (T1), Warm-Temperate (T2) and Cold-Temperate (T3)	4 Be	Warm region (T4), Cold-Temperate (T3) and Argentinean shelf-break I and II (T5-6)	4 Be	Tropical (T1), Rio Grande province (T7), Uruguay-Buenos Aires Shelf (T8) and Cold-Temperate (T3)
Benthic analysis	19 Be	Tropical (B1) and Warm-Temperate (B2)	3 Be	Tropical (B1), Warm-Temperate (B2) and Argentinean shelf-break I (B3)	3 Be	Tropical (B1), Warm-Temperate (B2) and Argentinean shelf-break I (B3)
Pelagic analysis	9 Be	Warm Region (P1), and Cold-Temperate (P2)	3 Be	Warm region (P1), Cold-Temperate (P2) and Argentinean shelf-break II (P3)	1 Be	Warm region (P1)
Benthopelagic analysis	31 Be	tropical (BP1), Warm region (BP2), Cold-temperate (BP3)	2 Be	Warm region (BP2) and Cold-Temperate (BP3)	X	

APPENDIXES

Appendix 1. Hydrozoan species analyzed (Leptothecata, Anthoathecata, Limnomedusae, Narcomedusae, Trachymedusae), and their respective life-cycle strategies. "m" for benthopelagic means "medusoid".

Species	**Benthic**	**Pelagic**	**Benthopelagic**
Clytia lomae			x
Clytia simplex			x
Amphinema dinema			x
Aequorea coerulescens			x
Aequorea forskalea			x
Aequorea macrodactyla			x
Amphinema rugosum			x
Asyncoryne ryniensis			x
Blackfordia virginica			x
Bougainvillia frondosa			x
Bougainvillia macloviana			x
Bougainvillia muscoides			x
Bougainvillia muscus			x
Bougainvillia pagesi			x
Bougainvillia rugosa			x
Cirrholovenia tetranema			x
Cladonema radiatum			x
Clytia gracilis			x
Clytia hemisphaerica			x
Clytia hummelincki			x
Clytia linearis			x
Clytia noliformis			x
Corymorpha forbesi			x
Corymorpha gigantea			x
Corymorpha gracilis			x
Corymorpha januarii			x
Coryne eximia			x
Coryne nipponica			x
Coryne producta			x
Cytaeis tetrastyla			x
Dipurena reesi			x
Ectopleura dumortierii			x
Ectopleura obypa			x

Euphysa aurata			x
Eutima coerulea			x
Eutima mira			x
Eutima sapinhoa			x
Gonionemus vertens			x
Halitiara formosa			x
Hebella scandens			x
Hybocodon chilensis			x
Hybocodon unicus			x
Hydractinia borealis			x
Hydractinia carica			x
Hydractinia uniformis			x
Lafoeina amirantensis			x
Laodicea undulata			x
Leuckartiara octona			x
Lovenella cirrata			x
Lovenella gracilis			x
Merga tergestina			x
Mitrocomella brownei			x
Mitrocomella polydiademata			x
Mitrocomella frigida			x
Modeeria rotunda			x
Obelia bidentata			x
Obelia dichotoma			x
Obelia geniculata			x
Olindias sambaquiensis			x
Proboscidactyla ornata			x
Proboscidactyla mutabilis			x
Ralpharia sanctisebastiani			x
Rathkea formosissima			x
Staurophora mertensii			x
Stylactaria hooperi			x
Turritopsis nutricola			x
Zanclea costata			x
Aglauropsis conanti		x	
Aglauropsis kawari		x	
Annatiara affinis		x	
Cirrhitiara superba		x	
Cosmetirella davisi		x	
Eucheilota duodecimalis		x	
Eucheilota ventricularis		x	

Eucodonium brownei		x	
Eutonina scintillans		x	
Gossea brachymera		x	
Halicreas minimun		x	
Halitholus intermedius		x	
Halopsis ocellata		x	
Laodicea pulchra		x	
Malagazzia carolinae		x	
Margelopsis australis		x	
Niobia dendrotentaculata		x	
Phialella falklandica		x	
Phialopsis diegensis		x	
Porpita porpita		x	
Protiaropsis anonyma		x	
Rhabdon singulare		x	
Rhancostoma atlantica		x	
Staurocladia vallentini		x	
Tiaricodon coeruleus		x	
Vallentinia falklandica		x	
Velella velella		x	
Aegina citrea		x	
Aglaura hemistoma		x	
Amphogona apicata		x	
Amphogona apsteini		x	
Colobonema sericeum		x	
Crossota brunnea		x	
Cunina duplicata		x	
Cunina frugifera		x	
Cunina octonaria		x	
Cunina peregrina		x	
Geryonia proboscidalis		x	
Halitrephes maasi		x	
Liriope tetraphylla		x	
Pegantha laevis		x	
Persa incolorata		x	
Rhopalonema velatum		x	
Sminthea eurygaster		x	
Solmaris corona		x	
Solmundella bitentaculata		x	
?Nemertesia ciliata	x		
Acryptolaria conferta	x		

Aglaophenia acacia	x		
Aglaophenia latecarinata	x		
Aglaophenia rhynchocarpa	x		
Aglaophenia trifida	x		
Amphisbetia operculata	x		m
Antennella secundaria	x		
Bimeria vestita	x		
Campanularia agas	x		
Campanularia hincksii	x		
Campanularia subantarctica	x		
Cladocoryne floccosa	x		m
Corydendrum parasiticum	x		
Cryptolarella abyssicola	x		
Dentitheca bidentata	x		
Diphasia digitalis	x		
Diphasia tropica	x		
Dynamena crisioides	x		
Dynamena dalmasi	x		
Dynamena disticha	x		
Dynamena quadridentata	x		
Eudendrium capillare	x		
Eudendrium caraiuru	x		
Eudendrium carneum	x		
Eudendrium merulum	x		
Eudendrium pocaruquarum	x		
Eudendrium ramosum	x		
Filellum contortum	x		
Gonothyraea loveni	x		m
Grammaria magellanica	x		
Gymnangium allmani	x		
Halecium beanii	x		
Halecium bermudense	x		
Halecium delicatulum	x		
Halecium dichotomum	x		
Halecium dyssymetrum	x		
Halecium lightbourni	x		
Halecium tenellum	x		
Halopteris carinata	x		
Halopteris constricta	x		
Halopteris diaphana	x		
Halopteris polymorpha	x		

Hartlaubella gelatinosa	x		
Hincksella cylindrica	x		
Idiellana pristis	x		
Lafoea coalescens	x		
Lafoea dumosa	x		
Lytocarpia canepa	x		
Lytocarpia tridentata	x		
Macrorhynchia grandis	x		
Macrorhynchia philippina	x		
Monostaechas quadridens	x		
Monotheca margaretta	x		
Monotheca pulchella	x		
Nemalecium lighti	x		
Nemertesia ramosa	x		
Opercularella belgicae	x		
Orthopyxis integra	x		m
Orthopyxis sargassicola	x		m
Parascyphus repens	x		
Parawrightia robusta	x		
Pennaria disticha	x		m
Phialella chilensis	x		m
Ectopleura crocea	x		m
Plumularia floridana	x		
Plumularia insignis	x		
Plumularia setacea	x		
Plumularia strictocarpa	x		
Pycnotheca mirabilis	x		
Rhizogeton nudus	x		
Salacia desmoides	x		
Scandia mutabilis	x		
Sertularella ?polyzonias	x		
Sertularella areyi	x		
Sertularella conica	x		
Sertularella cylindritheca	x		
Sertularella leiocarpa	x		
Sertularella mediterranea	x		
Sertularella tenella	x		
Sertularia distans	x		
Sertularia loculosa	x		
Sertularia marginata	x		
Sertularia notabilis	x		

Sertularia rugosissima	x		
Sertularia tumida	x		
Sertularia turbinata	x		
Stegopoma irregularis	x		
Symplectoscyphus flexilis	x		
Symplectoscyphus magellanicus	x		
Symplectoscyphus milneanus	x		
Symplectoscyphus subdichotomus	x		
Synthecium robustum	x		
Synthecium tubithecum	x		
Thyroscyphus marginatus	x		
Thyroscyphus ramosus	x		
Tulpa tulipifera	x		
Ventromma halecioides	x		
Zygophylax infundibulum	x		
Zygophylax sibogae	x		
Zyzzyzus warreni	x		

Appendix 2. Species supporting regions with higher endemicity scores resulting from Endemicity Analysis (EA) for Concatenated, Benthic, Pelagic, and Benthopelagic data matrices.

Analysis	**Region**	**Species**
Concatenated analysis	Tropical	*Aglaophenia latecarinata, Aglaophenia trifida, Bougainvillia rugosa, Campanularia hincksii, Cladocoryne floccosa, Clytia hummelincki, Clytia linearis, Clytia noliformis, Dentitheca bidentata, Diphasia tropica, Dynamena crisioides, Dynamena dalmasi, Dynamena quadridentata, Eudendrium carneum, Eudendrium pocaruquarum, Ectopleura dumortierii, Halecium bermudense, Halecium dyssymetrum, Halecium lightbourni, Halecium tenellum, Halopteris diaphana, Halopteris polymorpha, Hincksella cylindrica, Idiellana pristis, Lafoeina amirantensis, Lytocarpia tridentata, Macrorhynchia philippina, Monotheca margaretta, Nemalecium lighti, Orthopyxis integra, Orthopyxis sargassicola, Parawrightia robusta, Pennaria disticha, Pycnotheca mirabilis, Plumularia floridana, Scandia mutabilis, Sertularella areyi, Sertularia distans, Sertularia loculosa, Sertularia marginata, Sertularia rugosissima, Sertularia tumida, Sertularia turbinata, Synthecium tubithecum, Thyroscyphus ramosus, Ventromma halecioides, Zanclea costata, Zyzzyzus warreni, Proboscidactyla ornata, Cytaeis tetrastyla, Cirrholovenia tetranema, Eucheilota duodecimalis, Lovenella cirrata, Cunina peregrina, Solmaris corona, Aglaura hemistoma*
	Warm-Temperate	*Aglaophenia acacia, Amphinema dinema, Aequorea coerulescens, Campanularia agas, Grammaria magellanica, Halecium beanii, Hartlaubella gelatinosa, Laodicea undulata, Lytocarpia canepa, Halitiara formosa, Mitrocomella brownei, Monotheca pulchella, Opercularella belgicae, Phialella chilensis, Plumularia insignis, Stegopoma irregularis, Synthecium robustum, Tulpa tulipifera, Bougainvillia pagesi, Amphinema dinema, Clytia lomae, Clytia hemisphaerica, Eutima mira, Hybocodon chilensis, Malagazzia carolinae, Olindias sambaquiensis, Aglauropsis kawari*
	Cold-Temperate	*Bougainvillia macloviana, Hydractinia carica, Rathkea formosissima, Tiaricodon coeruleus, Loadicea pulchra, Halopsis ocellata, Halicrea minimun, Phialella falklandica, Aequorea macrodactyla, Aglauropsis conanti, Amphogona apicata*

Analysis	**Region**	**Species**
Benthic analysis	Tropical	*Aglaophenia latecarinata, Aglaophenia trifida, Campanularia hincksii, Dentitheca bidentata, Diphasia tropica, Dynamena crisioides, Dynamena quadridentata, Dynamena dalmasi, Eudendrium carneum, Eudendrium pocaruquarum, Halecium bermudense, Halecium dyssymetrum, Halecium lightbourni, Halecium tenellum, Halopteris diaphana, Halopteris polymorpha, Idiellana pristis, Hincksella cylindrica, Lytocarpia tridentata, Monotheca margaretta, Nemalecium lighti, Parawrightia robusta, Plumularia floridana, Pycnotheca mirabilis, Scandia mutabilis, Sertularella areyi, Sertularia distans, Sertularia loculosa, Sertularia marginata, Sertularia rugosissima, Sertularia turbinata, Sertularia tumida, Synthecium tubithecum, Thyroscyphus ramosus, Ventromma halecioides, Zyzzyzus warreni, Macrorhynchia philippina*
	Warm-Temperate	*Aglaophenia acacia, Campanularia agas, Grammaria magellanica, Halecium beanii, Lytocarpia canepa, Monotheca pulchella, Opercularella belgicae, Stegopoma irregularis, Synthecium robustum*
Pelagic analysis	Warm Region	*Cirrhitiara superba, Eucheilota duodecimalis, Aglauropsis kawari, Malagazzia carolinae, Niobia dendrotentaculata, Philopsis diegensis, Porpita porpita, Rhancostoma atlantica, Velella velella, Liriope tetraphylla, Aegina citrea, Aglaura hemistoma, Cunina peregrina, Solmaris corona*
	Cold-Temperate	*Aglauropsis conanti, Halicrea minimun, Halopsis ocellata, Laodicea pulchra, Phialella falklandica, Tiaricodon coeruleus*
Benthopelagic analysis	Tropical	*Clytia hummelincki, Clytia linearis, Clytia noliformis, Cirrholovenia tetranema, Cytaeis tetrastyla, Bougainvillia rugosa, Ectopleura dumortierii, Lafoeina amirantensis, Lovenella cirrata, Proboscidactyla ornata, Cladocoryne floccosa, Orthopyxis integra, Orthopyxis sargassicola, Pennaria disticha, Zanclea costata*
	Warm Region	*Blackfordia virginica, Clytia hemisphaerica, Clytia gracilis, Bougainvilla frondosa, Bougainvillia muscus, Cirrholovenia tetranema, Corymorpha januarii, Corymorpha gracilis, Corymorfa forbesi, Ectopleura dumortierii, Hebella scandens, Laodicea undulata, Obelia dichotoma, Olindias sambaquiensis, Proboscidactyla ornata, Orthopyxis sargassicola, Turritopsis nutricula, Dupurena reesi, Zanclea costata*
	Cold-Temperate	*Hydractinia carica, Rathkea formisissima*

Appendix 3 Species supporting biotic elements found by Three-Item Analysis of Distributions (3ID).

Analysis	Region	Species	Nested areas
Concatenated analysis	Warm Region	*Clytia gracilis*	Tropical: *Lafoeina amirantensis, Eudendrium carneum*, Warm-Temperate: *Clytia lomae*
	Cold-Temperate	*Laodicea pulchra*	
	Argentinean shelf-break I	*Cunina duplicata*	
	Argentinean shelf-break II	*Tulpa tulipifera*	
Benthic analysis	Tropical	*Eudendrium carneum*	
	Warm-Temperate	*Aglaophenia acacia*	*Campanularia agas*
	Argentinean shelf-break I	*Tulpa tulipifera*	
Pelagic analysis	Warm Region	*Liriope tetraphylla*	*Cunina peregrina, Cirrihitiara superba*
	Cold-Temperate	*Phialella falklandica*	
	Argentinean shelf-break II	*Cunina duplicata*	
Benthopelagic analysis	Warm Region	*Bougainvillia muscus*	Tropical: *Clytia linearis, Pennaria disticha* Warm-Temperate: *Halitiara formosa*
	Cold-Temperate	*Hydractinia carica,* *Rathkea formosissima*	

Appendix 4 Species supporting biotic elements found in Parsimony Analysis of Endemicity (PAE).

Analysis	**Region**	**Species**	**Nested areas**
Concatenated analysis	Tropical	*Clytia linearis*, *Dynamena crisioides*, *Halecium dyssymetrum*, *Monotheca margaretta*, *Pennaria disticha*, *Sertularia marginata*, *Ventromma halecioides*	
	Rio Grande province	*Cirrhitiara superba*	
	Uruguay-Buenos Aires Shelf	*Eutima mira*	
	Cold-Temperate	*Laodicea pulchra*	
Benthic analysis	Tropical	*Dynamena crisioides*, *Monotheca margaretta*, *Sertularia marginata*, *Ventromma halecioides*	
	Warm-Temperate	*Synthecium robustum*	
	Argentinean shelf-break I	*Tulpa tulipifera*	
Pelagic analysis	Warm Region	*Solmaris corona*	*Cirrhitiara superba*

Capítulo 4

Considerações finais

As pesquisas em biogeografia buscam utilizar o maior número possível de dados de distribuição dos táxons para gerar a melhor hipótese de áreas de endemismo. Porém, em uma comparação de métodos de análises de endemismo, conjuntos de dados reais apresentam uma avaliação limitada das diferenças metodológicas, ignorando-se como podem ser afetados por idiossincrasias da distribuição e propriedades intrínsecas dos métodos (Casagrande, 2012). Desta forma, a avaliação de uma metodologia de interesse deve incluir tanto conjuntos de dados hipotéticos como reais. Neste estudo, comparamos uma nova metodologia para encontrar áreas de endemismo, a Análise de Distribuições de Três-Itens (3ID) com os métodos mais utilizados em análises dessa natureza, *viz.*, a Análise de Parcimônia de Endemicidade (PAE, Morrone, 1994) e a Análise de Endemicidade (EA, Szumik *et al.*, 2002; Szumik & Goloboff, 2004), com base em dados hipotéticos e reais. Os resultados em geral revelam que 3ID é uma metodologia eficiente para diferentes casos de incongruência para dados hipotéticos e conjunto de dados reais de Hydrozoa do Oceano Atlântico Sul-Ocidental (OASO).

A análise dos 43 padrões de distribuição hipotéticos revelou que a EA é o único método confiável para recuperar um par de áreas sobrepostas, porém tem o pior desempenho para encontrar padrões aninhados. A PAE é o método com o pior desempenho em casos de sobreposição e um desempenho intermediário em casos de áreas aninhadas. Finalmente, a 3ID teve o melhor desempenho para recuperar áreas aninhadas e um desempenho intermediário em casos de áreas sobrepostas. Portanto, a melhor opção disponível para uma análise de endemismo é usar a 3ID e a EA de maneira complementar, aumentando assim a possibilidade de resolver os dois tipos de incongruência (sobreposição ou áreas aninhadas).

As análises com a distribuição real de 214 espécies de Hydrozoa do Oceano Atlântico Sul-Ocidental (OASO) revelaram três padrões principais no OASO: (1) Tropical, (2) Temperado-Quente e (3) Temperado-Frio, todos congruentes com propostas biogeográficas anteriores (i.e, Briggs & Bowen, 2012; Spalding et al., 2007). Nossos dados também corroboram que a delimitação de elementos bióticos em habitats marinhos varia de acordo com as diferentes estratégias de ciclos de vida de hidrozoários (Gibbons, 2010), assim como pode acontecer na biogeografia de qualquer outro táxon com ciclo de vida complexo. Igualmente, observamos que a EA e a 3ID obtiveram resultados mais consistentes e completos, corroborando o observado em com cenários predefinidos, e portanto recomendamos a utilização dessas duas metodologias em conjunto.

Análises semelhantes às nossas, explorando outras propriedades dos dados, como vieses amostrais, podem gerar uma compreensão mais profunda do comportamento do algoritmo proposto quando comparado a outras metodologias. Dado o aumento da informação sobre a distribuição das espécies marinhas, e a dificuldade das análises neste ambiente devido ao fato de não apresentarem barreiras evidentes, aperfeiçoamentos metodológicos para descrições mais realistas e robustas dos padrões biogeográficos marinhos permitirão um melhor embasamento para compreensão de cenários biogeográficos marinhos.

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Abstract

Areas of endemism or biotic elements comprise regions delimited by more than one taxon with coincident patterns of distribution. There is not an accepted universal protocol for delimitation of areas of endemism, and therefore, they are identified by several different methods. In this study, we propose an integrative comparison of different methods for identification of areas of endemism based on data of hypothetical and real distributions. Therefore, the general aims of this study are: (1) to compare the Parsimony Analysis of Endemicity (PAE), the Endemicity Analysis (EA) and a new coding method that we propose, the Three-Item Analysis of Distributions (3ID) to contrast their performance based on their ability to identify hypothetical predefined areas of endemism representing non-conflicting, nested and overlapping patterns; (2) to analyze the patterns of distribution of benthic, pelagic and benthopelagic non-siphonophore hydrozoans of the Southwestern Atlantic Ocean (SWAO), to test previous biogeographic hypotheses of regionalization for the area and to evaluate the performance of the endemicity methods based on real datasets.

In chapter 2, entitled “Comparison of analysis of endemism procedures based on hypothetical distributions”, we compared the performance of PAE, EA and 3ID, and we found that 3ID has the greatest percentage of success in retrieving predefined areas of endemism. EA is the only method that recovers overlapping patterns, but it can also find spurious patterns. We recommend the use of 3ID together with EA as the best available option for hypothesizing areas of endemism.

In chapter 3, entitled “Biogeographic patterns of benthic and planktonic hydrozoans from the southwestern Atlantic Ocean”, we used the distribution 214 hydrozoan species from the SWAO (20°-60°S, 33°-75°W), which were organized in different data matrices (concatenated, benthic, pelagic, and benthopelagic) according to the different life cycle strategies in Hydrozoa. All matrices were analyzed through PAE, EA and 3ID. The resulting areas showed three broad biogeographic patterns: (1) Tropical, (2) Warm-Temperate and (3) Cold-Temperate. The output patterns varied according to the life cycle of hydrozoan species, demonstrating the importance in analyzing separately data of species with different strategies of life cycle. Each method performed differently, and we concluded that the use of 3ID and EA together is the best approach to infer strong biogeographic patterns for the marine realm.

Resumo

Área de endemismo ou elemento biótico é uma região geográfica que apresenta congruência distribucional entre táxons. Não há um padrão aceito universalmente para delimitação de áreas de endemismo e, portanto, várias metodologias são usadas para sua identificação. Nesta dissertação, propomos uma comparação integrada de alguns métodos de análises de endemismo, com base em dados de distribuição hipotéticos e reais. Desta forma, este estudo tem como objetivos: (1) comparar a Análise de Parcimônia de endemicidade (PAE), a Análise de endemicidade (EA) e um novo método de codificação que propomos a Análise de Distribuições de Três-Itens (3ID), avaliando sua performance com base na capacidade de identificar padrões hipotéticos predefinidos de áreas de endemismo, representando áreas não conflitantes, aninhadas e sobrepostas; (2) analisar os padrões de distribuição de 214 espécies de hidrozoários bentônicos, pelágicos e benthopelágicos não-sifonóforos do Oceano Atlântico Sul Ocidental (OASO), usando três métodos biogeográficos para testar hipóteses anteriores de regionalização biogeográfica e avaliar o performance da PAE, a EA e a 3ID com conjuntos de dados reais.

No capítulo 2, intitulado “Comparison of analysis of endemism procedures based on hypothetical distributions”, nós comparamos a PAE, EA e 3ID e encontramos que a 3ID tem o maior percentual de sucesso na recuperação de áreas de endemismo predefinidas. Adicionalmente, a EA é o único método capaz de recuperar padrões sobrepostos, porém também encontra padrões espúrios. Nós sugerimos, portanto, que a melhor opção para identificação de áreas de endemismo é o uso de 3ID e EA em conjunto.

No capítulo 3, intitulado “Biogeographic patterns of benthic and planktonic hydrozoans from the southwestern Atlantic Ocean”, nós utilizamos dados distribucionais de 214 espécies de hidrozoários bentônicos, pelágicos e bentopelágicos não-sifonóforos do OASO (20°-60°S, 33°-75°W), os quais foram organizados em

diferentes matrizes (concatenada, bentônica, pelágica, e bentopelágica) de acordo com as diferentes estratégias de ciclo de vida em Hydrozoa. Todas as matrizes foram analisadas por meio da PAE, EA e 3ID. Os resultados mostram três padrões biogeográficos gerais: (1) Tropical (2) Temperado-Quente, e (3) Temperado-Frio. Os padrões obtidos variam de acordo com o tipo de ciclo de vida em Hydrozoa, demonstrando a importância de analisar-se separadamente conjuntos de dados de espécies com diferentes estratégias de reprodução. Cada método teve um desempenho diferente e, portanto, concluímos que o uso de 3ID e EA em conjunto é a melhor opção para inferir padrões biogeográficos marinhos.