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1 Original Article

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3 Reproductive strategy as a piece of the biogeographic puzzle: a case study using Antarctic  
4 sea stars (Echinodermata, Asteroidea)

5

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7

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## 37 **ABSTRACT**

38 Aim: To describe and analyse asteroid biogeographical patterns in the Southern Ocean (SO) and test whether  
39 reproductive strategy (brooder versus broadcaster) can explain distribution patterns at the scale of the entire  
40 class. We hypothesize that brooding and broadcasting species display different biogeographic patterns.

41

42 Location: Southern Ocean, south of 45°S

43

44 Methods: Over 14,000 asteroid occurrences are analysed using bootstrapped spanning network (BSN),  
45 nonmetrical multidimensional scaling (nMDS) and clustering to uncover the spatial structure of faunal similarities  
46 amongst 25 bioregions.

47

48 Results: Main biogeographical patterns are congruent with previous works based on other taxa and highlight the  
49 isolation of New Zealand, the high richness in the Scotia Arc area particularly of brooding species, an East / West  
50 Antarctic differentiation, and the faunal affinities between South America and sub-Antarctic Islands. Asteroids  
51 show lower endemism levels than previously reported with 29% of species occurring in Antarctica only. In  
52 particular, asteroids from Tierra del Fuego showed affinities with those of West Antarctica at the species level,  
53 suggesting a recent mixing of assemblages. Biogeographic patterns are highly linked to reproductive strategy.  
54 Patterns also differ according to the taxonomic level, revealing the underlying role of historical factors.

55

56 Main conclusions: Patterns of sea star biogeography are consistent with results obtained for other marine groups  
57 and are strongly linked to reproductive strategy.

58

59 Keywords: Antarctica, Benthos, Biogeographic Barrier, Echinodermata, Invertebrate, Regionalisation,  
60 Reproductive mode, Sea stars, Southern Ocean

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63

## 64 **INTRODUCTION**

65

66 The Southern Ocean *sensu lato* (SO), as defined by oceanographers, includes the marine area south of the  
67 Subtropical Front (STF) (Longhurst, 2007; Rintoul, 2007; Post *et al.* in De Broyer *et al.*, 2014). In the framework of  
68 large scale biogeographical studies of marine benthic life, the SO is generally divided into four major geographic

69 entities (i.e. provinces): the Magellanic Plateau, represented by the southern tip of South America (South Chile,  
70 South Argentina, Tierra Del Fuego and the Malvinas / Falkland Islands); Southern New Zealand, represented by  
71 the Campbell Plateau; the sub-Antarctic area, located between the STF in the north and the Polar Front (PF) in  
72 the south, which is mainly composed of abyssal plains and several igneous Islands (e.g. Crozet archipelago,  
73 Kerguelen and Heard Islands); and the Antarctic, defined as the region south of the PF (Griffiths *et al.*, 2009). The  
74 Antarctic province is one of the most remote places on Earth, despite representing ~11% of the global continental  
75 shelf surface, and surrounded by the SO which surface accounts for ~8% of all the world's oceans (Griffiths,  
76 2010; Ingels *et al.*, 2012). Each of these provinces can then be divided into smaller entities, defined as bioregions  
77 (cf. Hedgpeth 1969).

78         The long-term faunal connections within and among these four provinces cannot be explained by a “one  
79 size fits all” biogeographic theory. Indeed, biogeographic patterns appear to be dependent upon the taxon  
80 investigated (e.g. Barnes and Griffiths, 2007 for Bryozoa; Griffiths *et al.*, 2009 for Mollusca and Bryozoa; Downey  
81 *et al.*, 2012 for Porifera). All large-scale studies on biogeographic patterns of the SO benthic life indicate that  
82 oceanographic and historical factors have played a significant role in the current patterns (Linse *et al.*, 2006;  
83 Barnes and Griffiths, 2007; Downey *et al.*, 2012; Pierrat *et al.*, 2013). Oceanographic features which are unique to  
84 the SO, such as the PF, act as a barrier between polar and sub-Antarctic water masses. Both water masses show  
85 contrasting physico-chemical properties, and the PF creates a steep gradient in temperature and salinity  
86 (Venables *et al.*, 2012). Geomorphological features, such as a “belt” of abyssal basins surrounding the Antarctic  
87 continent, have resulted in the biogeographic isolation of the Antarctic shelf, especially the benthos (see Clarke *et al.*  
88 *et al.*, 2005). The combined impacts of surface currents, the environmental characteristics of the SO, and the long-  
89 term gradual cooling and past glacial-interglacial cycles occurring during the Plio-Pleistocene, have driven  
90 biogeographic patterns (Gonzalez-Wevar *et al.*, 2012; Strugnell *et al.*, 2012). The development of the Antarctic  
91 Circumpolar Current (ACC) during the Eocene/Oligocene, has and continues to play a major role in the circum-  
92 Antarctic structure of environmental and biotic patterns by initiating a fast, clockwise transport of water, dispersing  
93 propagules around the entire Antarctic continent (Pearse *et al.*, 2009; Pierrat *et al.*, 2013; David & Saucède,  
94 2015).

95         Regional-scale processes may also shape biogeographical patterns. For instance, the PF has “marine  
96 corridors” connecting distinct regions (Clarke *et al.*, 2005; Barnes and Clarke, 2011). Other oceanographic  
97 features, such as regional-scale eddies, island archipelagos, seamounts or refugia during glacial cycles may also  
98 have influenced the distribution of benthic species (e.g. Barnes & Kuklinski, 2010). Despite this permeability,  
99 benthic fauna living south of the PF are highly adapted to polar environmental conditions (e.g. McClintock, 1994;  
100 Peck *et al.*, 2006) and interactions among all the factors mentioned above have resulted in apparently high levels  
101 of endemism in many benthic taxa of the SO. The recent Biogeographic Atlas of the Southern Ocean (De Broyer

102 *et al.*, 2014, and chapters herein) estimates 57% endemism for bivalves, 79% for gastropods, 64% for  
103 pycnogonids, 87% for isopods, 81% for tanaids, 51% for ascidians and 80% for cumaceans.

104 Sea stars (Asteroidea, Echinodermata) are common organisms living on the Antarctic seafloor with  
105 specimens found in diverse environments (Brandt *et al.*, 2007; Linse *et al.*, 2007a; Mah & Blake, 2012). High  
106 latitude asteroids have been studied since the late 19th century in the SO (e.g. Sladen, 1889) with hundreds of  
107 species recorded (latest checklist in Moreau *et al.*, 2015) and frequent checklists (e.g. Moles *et al.*, 2015).  
108 Moreover, there is a particularly high proportion of brooding sea stars in the SO (Poulin *et al.*, 2002; Pearse *et al.*,  
109 2009). Despite the potential importance of asteroids as ecosystem structuring agents (Mah & Blake, 2012;  
110 Lawrence, 2013), very few studies have assessed the overall distribution pattern of SO asteroid diversity (Danis *et*  
111 *al.*, 2014; Moles *et al.*, 2015) and the relative importance of each driving factor involved in the observed patterns  
112 has not yet been addressed.

113 In a recent update of the Register of Antarctic Marine species (RAMS), Moreau *et al.* (2015) reported a  
114 total of 295 species, representing more than 15% of the nearly 1,900 extant species of asteroids (Mah & Blake,  
115 2012). Initiatives such as RAMS and the World Register of Marine Species (WoRMS) enable the use of global  
116 data systems (e.g. Ocean Biogeographic Information System (OBIS - <http://www.iobis.org/>), Global Biodiversity  
117 Information Facility (GBIF - <http://www.gbif.org/>)) to compile hundreds of thousands georeferenced data entries  
118 (Costello *et al.*, 2013; Jossart *et al.*, 2015). Such extensive datasets can be used to address key biological  
119 questions, such as the origin and the structure of asteroid biogeographic patterns in the SO.

120 The objectives of this work are to describe and analyse asteroid biogeographical patterns in the  
121 Southern Ocean (SO) and test whether reproductive strategy (brooder versus broadcaster) can explain  
122 distribution patterns. Specifically, we hypothesize that the contrasting ability of asteroids to disperse (short-range  
123 for brooders and long-range for broadcasters) will generate contrasting biogeographic patterns.

124

## 125 **MATERIALS ANS METHODS**

126

### 127 **Area of interest**

128

129 The geographic area investigated in this study focuses on the SO, at latitudes higher than 45°S (Fig. 1). The SO  
130 was then subdivided into the following 25 bioregions based on several recent biogeographic studies (Linse *et al.*,  
131 2006; Clarke *et al.*, 2007; Spalding *et al.*, 2007; Pierrat *et al.*, 2013; De Broyer & Jażdżewska, 2014) and to take  
132 into account all occurrences data available for the SO asteroids (see Fig. 1.) Adélie Land (ALand); Antarctic  
133 Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is.  
134 (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet

135 Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie  
136 Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen  
137 Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South  
138 Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF)  
139 and Weddell Sea (WS).

140

#### 141 **Data analyses**

142

143 Cleaned data (See Appendix 1 for data sources and quality control) were compiled into a matrix providing  
144 information for each species on the bioregion and depth of occurrence. The dataset was used in its entirety for  
145 richness analyses. For biogeographic analyses, occurrences from depths lower than 1,500 m (abyssal domain  
146 and beyond) were excluded to only focus on shelf areas and on the upper slope. This depth range also includes  
147 shallow canyons and troughs. The main changes in faunal communities of the SO occur at around 1,500 m depth,  
148 deeper than elsewhere in the world's oceans (Brandt *et al.*, 2014). Bathymetric data were compiled using the  
149 GEBCO\_2014 grid ([www.gebco.net](http://www.gebco.net)). Analyses were performed at the genus and species levels. At the species  
150 level, brooding and broadcasting species were also investigated separately to test our working hypothesis (see  
151 Appendix 1 for sources regarding the reproductive strategy). Species accumulation curves were calculated to test  
152 the consistency of richness estimation using PRIMER 6 (Clarke & Gorley, 2006) with a focus on the first 250  
153 stations (Fig. 2a).

154

155 Three complementary approaches were used to quantitatively investigate faunal similarities between the 25  
156 bioregions. Two multivariate analyses, nonmetrical multidimensional scaling (nMDS) and clustering, were carried  
157 out using PRIMER 6 (Clarke & Gorley, 2006) and the Bray-Curtis coefficient (Bray & Curtis, 1957). A similarity  
158 percentage (SP) is given by the cluster analyses to measure similarities among bioregions or groups of  
159 bioregions. We also used the bootstrap spanning network (BSN) procedure to visualise nonmetric inter-  
160 assemblages similarity structure as a connected network. BSN allows the simultaneous identification of partially or  
161 totally nested patterns as well as gradational linear or reticulated biogeographical structures (see detailed  
162 description in Brayard *et al.*, 2007, 2009). These three methods can be used to identify transitional areas between  
163 bioregions and groups of bioregions in term of faunal similarities.

164

165 A dissimilarity matrix was calculated using the Bray-Curtis coefficient (Bray and Curtis, 1957). Following the BSN  
166 procedure (see Brayard *et al.*, 2007), similarity relationships were displayed as a connected network directly  
167 superimposed on geographical maps. Nodes of the network represent studied bioregions and the robustness of

168 each BSN link between nodes was evaluated by bootstrap replications (10,000 replicates were computed here). A  
169 bootstrap support values (BSV: i.e. a confidence interval) is obtained for each link between bioregions (see  
170 Brayard *et al.*, 2007, 2009 for details). When superimposed on geographical maps, the BSN provides an intuitive  
171 visualization, as well as a quantitative appraisal of faunal exchange pathways and biogeographical structures.  
172 BSNs were created with the software BSN 1.0 (Brayard *et al.*, 2007) and visualisations were created in PAJEK  
173 1.07 (Batagelj & Mrvar, 2005). In order to quantitatively compare BSN among different taxonomic levels and  
174 reproductive strategies, we built a triangular matrix by multiplying the BSV between bioregions for each of our four  
175 studied situations (genus level, species level, brooding, and broadcasting species). When two or more pathways  
176 were possible in the BSN, we kept the smallest value in order to reflect the highest similarity relationship. The  
177 bioregions Bount&Ant, Cam&Auc, ASBS and Mac were removed from correlation analyses because they were  
178 rarely connected to other bioregions in the BSN analyses. A Mantel test using the Spearman coefficient was used  
179 to measure correlations between the BSN structures. Finally, endemism levels of asteroid species were analysed  
180 by comparing the SO area dataset and the OBIS/GBIF occurrences for the rest of the world. Endemism within  
181 each bioregion was also quantified.

182

## 183 **RESULTS**

184

### 185 **Sampling effort, richness patterns and endemism**

186

187

188 There are clear differences in sampling effort intensity among the bioregions, ranging from 16 stations for both  
189 Queen Maud Land & Enderby Land (QML&EL) and Ob & Lena seamounts (Ob&Lena) to 993 stations for  
190 Campbell and Auckland Is. (Cam&Auc) (Table 1). Similar patterns can be observed for the number of  
191 occurrences (from 45 in the Davis Sea & Wilkes Land (DS&WL) to 2,259 in the Weddell Sea (WS)) and the  
192 richness at any taxonomic level (the number of orders, families, genera and species ranges from 4 to 7, 9 to 20,  
193 14 to 61, 20 to 128, respectively). Species accumulation curves for each bioregion (Fig. 2a, b) indicate that  
194 bioregions Cam&Auc, Ker and Ross are the only ones reaching an asymptote and that many species remain to  
195 be discovered in the SO regardless of the location. The steepest curves, reflecting potential high species  
196 richness, are all found in the area between South America and the Antarctic Continent (TdF, SG&Sha, SSand,  
197 SOrk, AP&SSh and WS). Our final dataset contained 14,005 occurrence records, accounting for 4,512 stations.  
198 All seven orders of the class Asteroidea were represented, including 299 species assigned to 28 families and 118  
199 genera (Table 1).

200

201 Of the 299 species in the dataset, 196 (~66%) also occur south of the PF and 123 species (~41%) have  
202 distributions that also extend north of the STF. Thus, a total of 176 species (~59%) occur exclusively south of the  
203 STF and are endemic to the Southern Ocean. Among the 196 species found south of the PF, 56 are restricted to  
204 the Antarctic zone (~29% endemism). In our dataset, 66 species (~22%) are only found around southern New  
205 Zealand and the adjacent regions (Chatham Islands, Tasmania), but not in any other region of the SO. At the  
206 scale of a bioregion endemism is low, varying from zero to four endemic species.

207

### 208 **Biogeographic patterns of species**

209

210 Bioregions are structured into three major groups (Fig. 3a, b): (I) the New Zealand province, composed of  
211 Bount&Ant and Cam&Auc bioregions (SP = 6% only with the closest bioregions); (II) South America and the sub-  
212 Antarctic Islands (SChi, SArg, Fal, Heard, Ker, Ob&Lena, Cro, PEd&Mar), and is separated from the third group at  
213 SP = 36%, and; (III) Antarctic bioregions (Bal&Sco, Bouv, PBay, Aland, Ross, AP&SSh, WS, SG&Sha, SOrk,  
214 SSand, QML&EL, DS&WL andTdF). Cluster analyses indicate that groups II and III can be subdivided into smaller  
215 geographic entities: South-America (IIa) and the sub-Antarctic Islands (IIb) (SP = 38%), East-Antarctic (bioregions  
216 east of the prime meridian, including Ross) (IIIa) and West Antarctic (bioregions west of the prime meridian) (IIIb)  
217 (SP = 52%), respectively. Potential faunal connections among these entities are highlighted by the BSN analysis  
218 (See Appendix 2 for BSV) (Fig. 3b). East and West Antarctica are well-connected to each other including a  
219 particularly strong link between the Weddell (WS) and Ross Seas (BSV = 100%) no link between WS and the  
220 closest other bioregions of East Antarctica. West Antarctica and South America are connected to each other  
221 through TdF (BSV = 99.9%). South America shows a strong link with the sub-Antarctic Islands (BSV = 99.8%).  
222 Within the sub-Antarctic group, the link is weak (BSV = 63%) between Macquarie and other sub-Antarctic Islands.

223

224 The nMDS analysis allows visualising similarities among bioregions with a low stress value (0.08). The minimum  
225 spanning tree (MST) plotted on the graph indicates the shortest path between bioregions (Fig. 4a, b) and confirms  
226 that bioregions from New Zealand are well differentiated from others. Two other bioregions, AS&BS and Mac, are  
227 also well discriminated. Other bioregions (Fig. 4b) are plotted together following a north-south differentiation: sub-  
228 Antarctic and South American bioregions on one side, Antarctic bioregions and the Scotia Arc on the other, with  
229 the exception of Tierra del Fuego that shows affinities with Antarctic bioregions (note the shortest path between  
230 TdF and SOrk).

231

### 232 **Brooders versus broadcasters**

233

234 Information about reproductive strategies was available for 59 species with occurrence data shallower than 1,500  
 235 m: 37 brooding species (accounting for 2,403 occurrences) and 22 broadcasting species (4,608 occurrences).  
 236 Cluster analysis of brooding species (Fig. 3e) indicates five groups: (I) Ob & Lena seamounts (Ob&Lena) and the  
 237 South Sandwich Island (SSand) (SP = 22% with the remaining groups); (II) sub-Antarctic Islands (Ker, Heard, Cro  
 238 and PEd&Mar) (SP = 24% with the remaining groups); (III), four New Zealand, sub-Antarctic and Antarctic  
 239 bioregions (Cam&Auc, Bal&Sco, Bouv and DS&WL); (IV) eight Antarctic bioregions (SP = 40% between group III  
 240 and IV) differ from the fifth group; (V) South American bioregions (SChi, Fal, SArg and TdF) at SP = 30%. The  
 241 Antarctic group is subdivided into two sub-groups: high Antarctic (IVa) (WS, PBay, ALand and Ross) and West  
 242 Antarctic (IVb) (SG&Sha, AP&SSh and SOrk) (SP = 59%). BSN connections (Fig. 3f) indicate the occurrence of a  
 243 link between New Zealand and Balleny & Scott Is. (Bal&Sco) (BSV = 86%) as well as strong affinities among all  
 244 bioregions of the high Antarctic (continental Antarctic excluding the Antarctic peninsula). South America is  
 245 strongly linked to the West Antarctic to the south and the sub-Antarctic Islands to the east through South Georgia  
 246 & Shag Rocks (SG&Sha) (BSV = 98.5% and 85.7% respectively).

247  
 248 Faunal affinities for broadcasting species (Fig. 3g) show higher similarity values than brooders, except for New  
 249 Zealand (I) which is isolated at 12% of SP. A second group (II) formed by Antarctic (AS&BS, QML&EL) and South  
 250 American bioregions (SChi, and SArg) is distinguished from the remaining bioregions (III) (SP = 46%) structured  
 251 into two subgroups (SP=64%): the sub-Antarctic Islands (IIIa) and Antarctic bioregions with TdF (IIIb). The BSN  
 252 network for broadcasting species (Fig. 3h) highlights the isolation of New Zealand from SO bioregions. Sub-  
 253 Antarctic Islands are all strongly linked to each other and to South America through Tierra del Fuego (TdF) (BSV  
 254 = 98.8%). Brooder and broadcaster networks (Table 2) were not correlated ( $r_s = 0.296$ ;  $p = 0.067$ ).

255

## 256 **Biogeographic patterns of genera**

257

258 At genus level, bioregions are structured in three distinct geographic groups (Fig. 3c, d): (I) New Zealand  
 259 (SP=32%), (II) South America (including TdF) and the sub-Antarctic Islands together, separated from a last group  
 260 composed of (III) Antarctic bioregions (SP = 55%). At regional scale, group II can be split into two smaller entities:  
 261 South America (IIa) and the sub-Antarctic Islands (IIb) (SP = 59%). The structure of Antarctic bioregions follows a  
 262 more complex pattern of three distinct sub-groups (SP = 65 to 70%): Antarctic Islands (IIIa) (Bal&Sco and Bouv),  
 263 West Antarctic bioregions (IIIb) (SG&Sha, AP&SSh and SOrk) and high Antarctic (IIIc) (Ross, WS, ALand and  
 264 PBay). BSN connections among these sub-groups (Fig. 3d) highlight the isolation of New Zealand from other  
 265 bioregions of the SO and in contrast, strong links between Antarctic bioregions. Bioregions of South America are  
 266 linked to West Antarctic through the South Orkney bioregion (BSV = 98.2%). Sub-Antarctic Islands are connected

267 to West Antarctic through South Georgia & Shag Rocks (Sg&Sha; BSV = 86%) to the west and to Macquarie  
268 Island (BSV = 66%) to the east. A strong circumpolar connection is present without the gap observed at species  
269 level between the Weddell Sea (WS) and the closest other bioregions of East Antarctica (BSV = 99.4%) (Fig. 3d).  
270 There is a significant correlation (Table 2) between genus and species networks ( $r_s = 0.728$ ;  $p < 0.0005$ ), between  
271 genus and brooder networks ( $r_s = 0.641$ ;  $p < 0.0005$ ), and a moderate but significant correlation between the  
272 genus and broadcaster networks ( $r_s = 0.444$ ;  $p = 0.0142$ ).

273

## 274 **DISCUSSION**

275

### 276 **Main patterns of SO asteroid biogeography**

277

278 At species level, high levels of endemism reflect the isolation of marine biogeographic units due to oceanographic  
279 barriers to dispersal or environmental filters. We found low values of endemism for each bioregion when  
280 considered in isolation in contrast to the high levels of endemism for the SO (59%) and Antarctic region (29%).  
281 These levels are similar to those previously reported for the SO (Moles *et al.*, 2015) and high compared to other  
282 regions, possibly due to the ancient isolation of the SO by the ACC front system associated to speciation and  
283 radiation events within Antarctic waters (Watling & Thurston, 1989; Lecointre *et al.* 2013; De Broyer &  
284 Jazdzewska, 2014).

285

286 Our quantitative analyses highlighted the relatively weak biogeographic connectivity of New Zealand to SO  
287 bioregions at all taxonomic levels and reproductive strategies. The influence of New Zealand cold temperate  
288 fauna on its southernmost areas is shown by the high level of endemism observed within and around New  
289 Zealand waters. The uniqueness of the New Zealand's benthic fauna compared to the rest of the SO benthos has  
290 been demonstrated in many studies on diverse taxa (e.g. molluscs: Linse *et al.*, 2006; bryozoans: Barnes &  
291 Griffiths, 2007; echinoids: Pierrat *et al.*, 2013).

292

293 The faunal affinities between East Antarctica and the Macquarie Island suggest that faunal connections may  
294 occur through the southern Macquarie ridge, as demonstrated for other echinoderms (asteroids and ophiuroids)  
295 (O'Hara, 1998; O'Hara *et al.*, 2013). An additional link was observed between Macquarie and the sub-Antarctic  
296 islands, supporting a pattern already established for echinoderms (asteroids, ophiuroids and holothuroids:  
297 O'Hara, 1998). Passive transport of adults and juveniles by kelp rafting may explain this affinity (Edgar, 1987) as  
298 well as a long distance transport of larvae.

299

300 Distribution patterns of asteroids are strongly structured within the SO. Antarctic and sub-Antarctic provinces are  
301 well-differentiated from each other with bioregions of East and West Antarctica grouped together to the south,  
302 bioregions of South America and the sub-Antarctic Islands to the north. Asteroid distribution is therefore strongly  
303 structured according to latitude. This may be a result of the PF acting as a biogeographic barrier to the dispersal  
304 of asteroids leading to distinct species assemblages between the two provinces. Northern bioregions are  
305 clustered together following an additional, longitudinal segregation between South American bioregions to the  
306 west and sub-Antarctic islands to the east.

307  
308 The role of the PF as a barrier to gene flow between Antarctic and sub-Antarctic benthic fauna has been  
309 frequently discussed (Clarke *et al.*, 2005; Fraser *et al.*, 2012), although it can be relatively permeable to certain  
310 species (Convey *et al.*, 2009; Sands *et al.*, 2015; Fraser *et al.*, 2016). This is supported by the BSN analyses  
311 where there is no obvious faunal connection between the sub-Antarctic and Antarctic bioregions, but through the  
312 Scotia Arc bioregions. This last area constitutes a potential gateway to Antarctica for northern fauna, as  
313 demonstrated in previous research (e.g. IBMANT: Arntz, 2005). Explanations for this include the role of  
314 mesoscale eddies (Glorioso *et al.*, 2005; Chown *et al.*, 2015) and stepping-stone dispersal through islands of the  
315 Scotia Arc (e.g. Tatiàn *et al.*, 2005; Fortes & Absalão, 2011). Our results also show faunal affinities between  
316 Magellanic and sub-Antarctic assemblages, supporting previous studies on sponges (Downey *et al.*, 2012),  
317 molluscs (Griffiths *et al.*, 2009) and echinoids (Pierrat *et al.*, 2013). This pattern is probably driven by the  
318 westward flowing ACC allowing long-distance dispersal of propagules (see Waters, 2008 for discussion).

319  
320 West and East Antarctica bioregions are well-differentiated from each other, confirming previous studies (e.g.  
321 Griffiths *et al.*, 2009; Pierrat *et al.*, 2013; De Broyer & Jażdżewska, 2014). Here, the geological/glacial history of  
322 Antarctica can be invoked as a possible cause as the Weddell, Amundsen and Ross Seas may have been  
323 connected by a trans-Antarctic seaway (Lawver & Gahagan, 2003; Pollard & DeConto, 2009) that separated East  
324 Antarctica from continental fragments of West Antarctica (Linse *et al.*, 2006; Pierrat *et al.*, 2013). Molecular  
325 studies partially support this hypothesis (Strugnell *et al.*, 2012), although data from East Antarctica are needed for  
326 confirmation. The east-west pattern may also have originated from the contrasting environmental conditions that  
327 prevail between East and West Antarctica (David & Saucède, 2015). The affinity of asteroid faunas between  
328 Tierra del Fuego and West Antarctic bioregions is a novel result, highlighting the importance of connections  
329 between South America and Antarctica.

330  
331 West Antarctic is surprisingly rich in asteroid species, even when compared to other well-sampled areas (Table 1;  
332 Fig. 2). As previously discussed (Barnes, 2005; Barnes *et al.*, 2006; Linse *et al.*, 2007b), this can be accounted for  
333 by the ACC hypothesis (see Pearse *et al.*, 2009) that suggests that recurrent (but sporadic) transport of brooding

334 species by the ACC caused their establishment in the Scotia Arc region. The hypothesis predicts the “existence of  
335 many species in clades of varied divergence times, at a wide range of depths, but with highest diversity  
336 downstream of the Drake Passage (passage between Cape Horn and the Antarctic peninsula), in the Scotia Arc  
337 and Weddell Sea” (Pearse *et al.*, 2009). Here, the high number of brooding species and strong species:genus  
338 ratio in the Scotia Arc area supports this hypothesis.

339

#### 340 **The importance of reproductive strategies for asteroid biogeography**

341

342 Pappalardo & Fernández (2014) recently reported a poleward increasing number of direct developers in  
343 crustaceans and molluscs. They linked this to low temperatures and food availability in the highest latitudes,  
344 emphasizing the importance of life history traits such as larval development in determining patterns of species  
345 richness in marine taxa. The high number of brooding asteroid species in the SO can also be explained by  
346 vicariance and allopatry, and not solely as a consequence of adaptation (Poulin *et al.*, 2002, Pearse *et al.*, 2009).

347

348 The ecological uniqueness of the New Zealand asteroid fauna can be explained by the geographic position of  
349 New Zealand, which limits faunal exchange and larval dispersal to the south. Surprisingly, with only three  
350 brooding species reported in New Zealand waters (among which two are found in the Antarctic region), our results  
351 show a connection with East Antarctica (Fig. 3f). This weak link might be an artefact due to the very small number  
352 of species, but could also reflect an existing relationship such as that proposed for cheilostomatid bryozoa  
353 (Griffiths *et al.* 2009).

354

355 The diversity of asteroids from the sub-Antarctic Islands region appears to have been shaped by a complex  
356 evolutionary history. Here, reproductive strategy significantly contributes to our understanding of large-scale  
357 distribution patterns. Asteroids of the sub-Antarctic Islands show fewer affinities with South American species than  
358 with those of both West and East Antarctic regions. The low capacity of brooders to disperse over large distances  
359 (around 7,000 km between South America and the sub-Antarctic Islands) partly explains this delineation, given  
360 the absence of stepping stones between the sub-Antarctic Islands. In contrast, the high dispersal capacity of  
361 broadcasters reduces the impact of geographic isolation on faunal exchange between provinces. In summary, an  
362 original fauna evolved *in situ* around the islands, with some species arriving from South America and others from  
363 the Antarctic region. This scenario explains the interrelationships of the fauna of Tierra del Fuego (Fig. 3h), which  
364 is highly influenced by both South America and the West Antarctica region. Only brooding species show a clear  
365 structuring of Antarctic bioregions. In contrast, broadcasting species show weak spatial structure with a clear  
366 circumpolar continuity and no distinct biogeographic boundary.

367  
368 More information is required to fully understand the role of reproductive strategy in asteroid biogeography. Larval  
369 ecology of sea stars in the SO takes a variety of different forms (Bosch & Pearse, 1990), with planktonic  
370 (planktotrophic or lecithotrophic) larvae for broadcasters. The pelagic larval duration may also vary among species,  
371 up to 165 days for *Odontaster validus* (Bosch & Pearse, 1990) which allows a huge potential for long-distance  
372 dispersal. Brooding biology also varies with some broods developing within suboral maternal brood chambers and  
373 others beginning their development in the stomach pouch (McClintock *et al.*, 2006). Broods can be carried for  
374 several months before releasing a fully developed juvenile. So far there has been little research on species in the  
375 SO (Agüera *et al.*, 2015), and most of this focuses on near-shore shallow-water species. Overall, brooders  
376 account for low fecundity, high survival and a limited dispersal capacity. On the contrary broadcasters have a high  
377 fecundity and a low survival rate of their larvae. Another potentially important (and understudied) factor is variation  
378 in habitat suitability for larvae along the dispersal routes. Such suitability depends on many factors including diet  
379 of larvae, the dynamics of planktonic life (Byrne *et al.*, 2016), substrate availability, and biotic interactions (i.e.  
380 competition). New modelling techniques based on experimental data (Dynamic Energy Budget – Functional Trait  
381 and Distribution Models) are starting to produce insights into these mechanisms, and can even generate  
382 predictive scenarios of migration or invasion (e.g. Byrne *et al.*, 2016).

383

#### 384 **Across taxonomic levels and time scales**

385

386 Analysing biogeographic patterns at high taxonomic levels can bring insights about upstream patterns of  
387 distribution and, in particular, the legacy of past processes for present-day biogeography (Pierrat *et al.*, 2013). Our  
388 genus-level analysis revealed that some SO distribution patterns are ancient and probably linked to major  
389 processes that occurred in the past. For instance, the Antarctic versus sub-Antarctic pattern is probably due to the  
390 long history of isolation of Antarctic waters. The setting up of the PF and of the ACC in the early Oligocene (30 Ma  
391 BP) (Lawver & Gahagan, 2003; Lawver *et al.*, 2014) and of other biogeographic barriers resulting from past  
392 geological activity were accompanied by vicariant processes. However, the use of molecular markers is needed to  
393 build robust phylogenies and increase the accuracy of divergence times between clades to infer the potential  
394 impact of past geological events on the evolution of the fauna. For example, González-Wevar *et al.* (2012) used  
395 the COI marker in various taxa (*Sterechinus*, *Nacella* and *Yoldia*) to demonstrate that the barrier between  
396 Antarctic and sub-Antarctic areas formed 3.7 to 5 Mya. This barrier reflects the recent impact of Plio-Pleistocene  
397 glaciations more than the ancient oceanographic history of the ACC. Janosik *et al.* (2011) drew a similar  
398 conclusion using data on asteroids, and proposed that mixing was still possible during the Last Glacial Maximum  
399 (21,000 years ago) due to changing and moving boundaries of the PF. In contrast, the molecular phylogeny of the

400 sea star superorder Valvatacea (Mah & Foltz, 2011a) suggests a possible ancestry of the Antarctic fauna from the  
401 adjacent sub-Antarctic regions and a diversification of the Antarctic Asteroidea associated with the isolation of the  
402 SO fauna and the formation of the ACC. Another molecular study on the asteroid superorder Forcipulatacea (Mah  
403 & Foltz, 2011b) also supports the hypothesis of diversification of Antarctic clades when the ACC first started to  
404 flow.

405  
406 At the generic level, the circum East Antarctic versus West Antarctic pattern can be accounted for by the  
407 existence of a past trans-Antarctic pathway linking the Weddell and Ross seas (Linse *et al.*, 2006; Pierrat *et al.*,  
408 2013). The closure of this pathway and the existence of the Weddell Sea Gyre might explain the absence of  
409 strong faunal similarities between the Weddell Sea and the close bioregions of East Antarctic at the species level  
410 (Linse *et al.*, 2006; Pierrat *et al.*, 2013). Finally, in contrast to the species level analysis, dissimilarities between  
411 the asteroid genera of Tierra del Fuego and the West Antarctic region might reflect the recent mixing of species  
412 between South America and West Antarctica.

413  
414 Surprisingly, the biogeographic patterns shown for brooding species are very similar to those of all asteroid  
415 genera. New Zealand apart, the two patterns fit almost perfectly and are statistically the most similar to each other  
416 (Table 2). This may simply illustrate the conservative biogeographic patterns of brooders compared to  
417 broadcasters that are able to disperse over long distances, which is supported by the circum-polar patterns shown  
418 in many species (35% of the species found south of the PF in this study) from many taxonomic groups. Such an  
419 ability to disperse may also explain the counter-intuitive presence of multiple lineages of certain circum-polar  
420 broadcasting species at the same locations (see Hemery *et al.*, 2012). If broadcasting species were isolated into  
421 refugia during glacial maxima, their populations may have evolved independently and merged again after  
422 conditions warmed to form the current biogeographic patterns.

423

## 424 **Conclusions**

425

426 The biogeographical patterns observed for sea stars in the SO are consistent with those of other taxonomic  
427 groups. Our result highlights the important role of reproductive strategy to understand large-scale spatial patterns  
428 of faunal distribution of asteroids. We therefore recommend that, whenever possible, reproductive strategy should  
429 be taken into account in large scale biogeographical studies. Finally, more effort is needed to fill data shortfalls  
430 and to date the diverse origins of biogeographic patterns in the SO. Using molecular tools in studies of asteroid  
431 species with contrasted reproductive strategies should bring new insights and help to gain a comprehensive  
432 understanding of historical legacy on present-day biogeography of the SO.

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666 **SUPPORTING INFORMATION**

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668 Additional Supporting Information may be found in the online version of this article:

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670 Appendix S1 Data source and quality control for Southern Ocean Asteroidea

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672 Appendix S2 Bootstrap Spanning Values for each Bootstrap Spanning Network

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674 Biosketch: **Camille Moreau** is a research scientist at the Université Libre de Bruxelles (ULB) and Université de Franche-Comté

675 (UFC). He focuses on distribution patterns of sea stars (Asteroidea) in the Southern Ocean and their origin.

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679 Author contribution: C.M., T.S. and B.D. led the writing; C.M., Q.J., A.A. and A.B. performed the analyses; C.M. collected the

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## TABLES AND FIGURES

Table 1 Breakdown numbers of occurrences, stations and taxonomic entities of Asteroidea for each of the 25 investigated bioregions. NA refers to occurrences found outside of the bioregions of interest. Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is. (Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS).

Bioregion	No. of occurrences	No. of species	No. of known brooding species	No. of known broadcasting species	No. of genera	No. of families	No. of orders	No. of stations	
ALand	694	47	12		14	30	15	7	141
AP&SSh	2042	128	25		18	61	20	7	618
AS&BS	49	21	7		4	16	9	6	31
Bal&Sco	202	34	4		15	28	15	6	78
Bount&Ant	245	47	1		2	35	14	7	149
Bouv	128	36	6		15	24	10	5	35
Cam&Auc	1586	80	3		6	53	19	7	993
Cro	489	46	5		9	27	15	5	118
DS&WL	45	20	6		7	14	9	4	26
Fal	232	47	8		9	31	17	6	70
Heard	223	31	6		8	20	14	6	85
Ker	1477	52	12		9	31	16	6	422
Mac	141	25	5		2	16	13	5	56
NA	673	126	NA		NA	73	24	7	234
Ob&Lena	68	21	2		8	15	12	5	16
PBay	284	44	10		13	31	15	7	106
PEd&Mar	106	36	5		7	25	14	5	29

QML&EL	111	30	5	9	21	11	6	16
Ross	1257	70	12	16	42	18	6	398
SArg	154	42	9	5	27	15	7	63
SChi	131	38	3	6	30	18	6	55
SG&Sha	405	66	17	16	43	19	7	155
SOrk	421	68	14	17	45	19	7	124
SSand	174	48	5	11	34	17	6	68
TdF	409	73	13	12	49	19	7	178
WS	2259	101	13	16	51	18	7	248
Southern Ocean	14005	299	37	22	118	28	7	4512

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Table 2 Results of the Mantel test between BSN structure matrices using the Spearman coefficient.  $r_s$  is the

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correlation value and  $p$  the associated probability. Significant values are followed by an asterisk ( $p < 0.05$ ).

Situation	$r_s$	$p$
Brooders vs Broadcasters	0.296	0.067
Brooders vs Genus	0.641*	0.0002
Broadcasters vs Genus	0.444*	0.0142
Genus vs Species	0.728*	0.0001

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729 Figure &amp; legends

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731 Fig. 1 Map of the Southern Ocean. Area of study (below 45°S) showing the bioregions: Adélie Land (ALand);

732 Antarctic Peninsula &amp; the South Shetland Is. (AP&amp;SSh); Amundsen &amp; Bellingshausen Sea (AS&amp;BS); Balleny &amp;

733 Scott Is. (Bal&amp;Sco); Bounty &amp; Antipodes Is.(Bount&amp;Ant); Bouvet Is. (Bouv); Campbell &amp; Auckland Is. (Cam&amp;Auc);

734 Crozet Is. (Cro); Davis Sea &amp; Wilkes Land (DS&amp;WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker);

735 Macquarie Is. (Mac); Ob &amp; Lena seamounts (Ob&amp;Lena); Prydz Bay (PBay); Prince Edward &amp; Marion Is.

736 (PEd&amp;Mar); Queen Maud Land &amp; Enderby Land (QML&amp;EL); Ross Sea (Ross); South Argentina (SArg); South

737 Chile (SChi); South Georgia &amp; Shag Rocks (SG&amp;Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand);

738 Tierra Del Fuego (TdF) and Weddell Sea (WS). Depth of study, between 0 and 1500m is shown in light grey.

739 Projection: South Pole stereographic

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741 Fig. 2 Accumulation curves at the species level of Asteroidea for each investigated bioregions: Adélie Land

742 (ALand); Antarctic Peninsula &amp; the South Shetland Is. (AP&amp;SSh); Amundsen &amp; Bellingshausen Sea (AS&amp;BS);

743 Balleny &amp; Scott Is. (Bal&amp;Sco); Bounty &amp; Antipodes Is.(Bount&amp;Ant); Bouvet Is. (Bouv); Campbell &amp; Auckland Is.

744 (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen  
 745 Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is.  
 746 (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South  
 747 Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand);  
 748 Tierra Del Fuego (TdF) and Weddell Sea (WS). (a) Close-up of the first 250 stations. (b) Complete dataset

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750 Fig. 3 Cluster analyses (average linkage) of the percentage faunal similarity (a, c, e and g) using the Bray-Curtis  
 751 index and bootstrapped spanning networks (b, d, f and h) performed for species and genus level as well as for  
 752 brooding and broadcasting species for the class Asteroidea among the studied bioregions: Adélie Land (ALand);  
 753 Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny &  
 754 Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc);  
 755 Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker);  
 756 Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is.  
 757 (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South  
 758 Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand);  
 759 Tierra Del Fuego (TdF) and Weddell Sea (WS). Links with BSV < 70% correspond to dashed lines, links with BSV  
 760 < 50% are not shown. Corresponding groups based on the cluster analyses display a similar colour. Green: New  
 761 Zealand – Red: South America – Orange: Sub-Antarctic Islands – Blue: High Antarctic or East-Antarctic – Purple:  
 762 West-Antarctic – Burgundy: Circumpolar Pattern.

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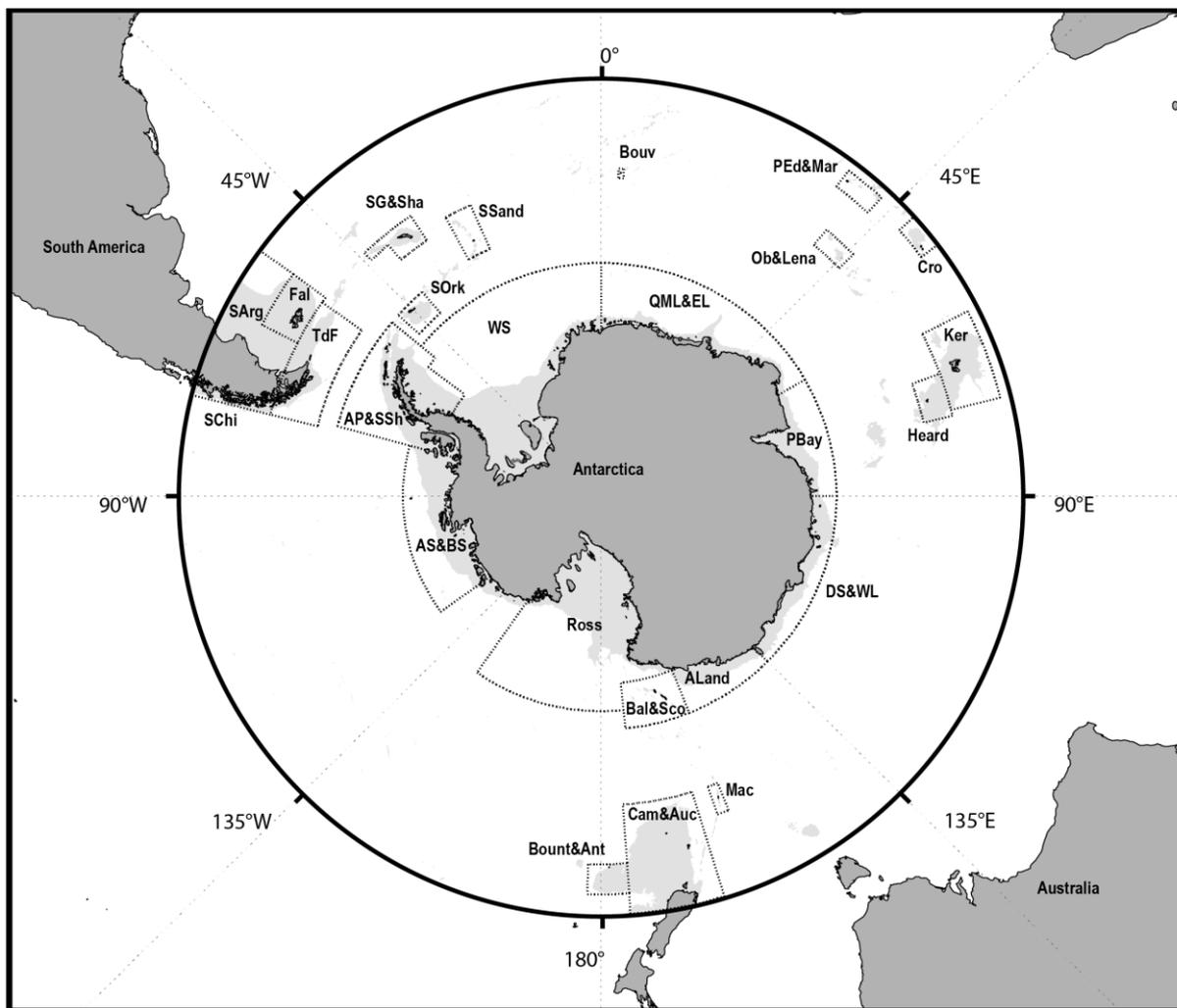
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765 Fig. 4 Nonmetric multidimensional scaling map with superimposed minimum spanning tree (partial representation  
 766 to ease the reading) for the class Asteroidea among the 25 studied bioregions: Adélie Land (ALand); Antarctic  
 767 Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is.  
 768 (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet  
 769 Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie  
 770 Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen  
 771 Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South  
 772 Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF)  
 773 and Weddell Sea (WS). (a) All bioregions (b) Close-up without AS&BS, Mac, Cam&Auc and Bount&Ant.

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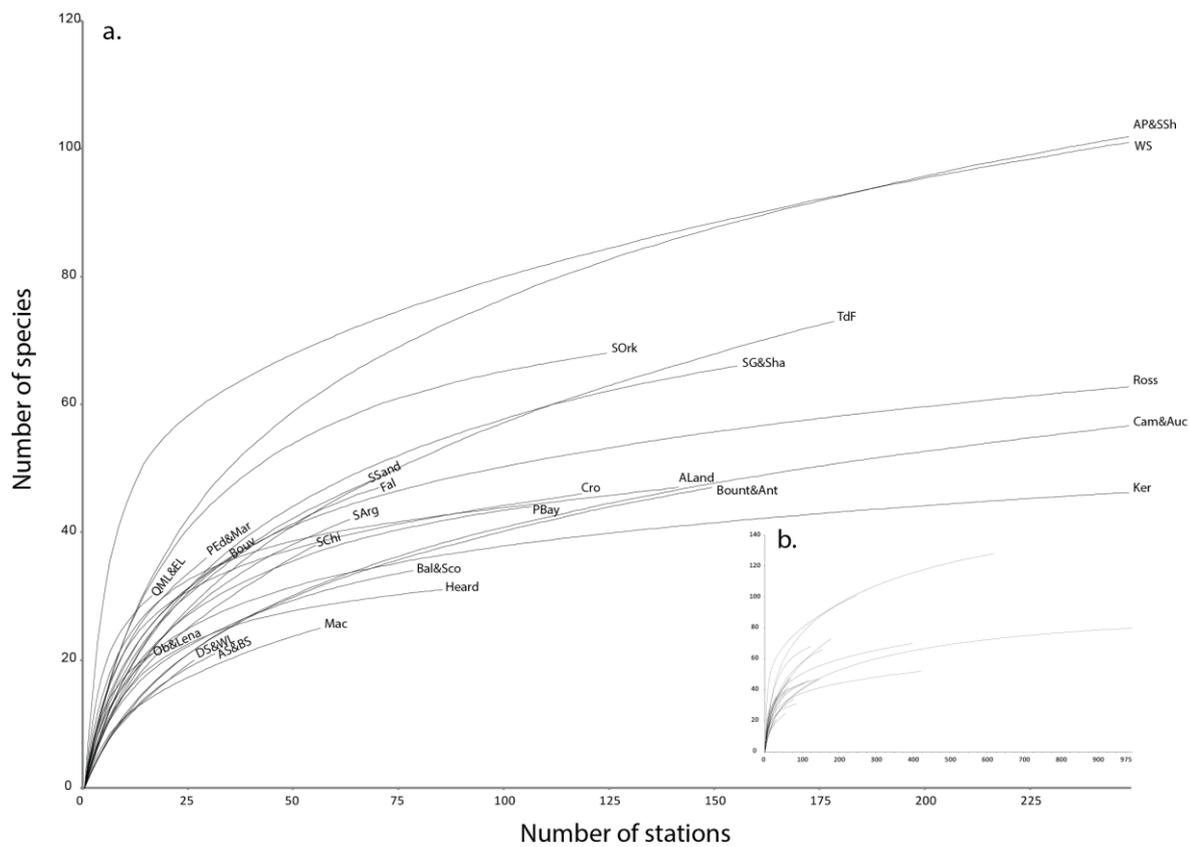
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776 Figure 1



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Figure 2

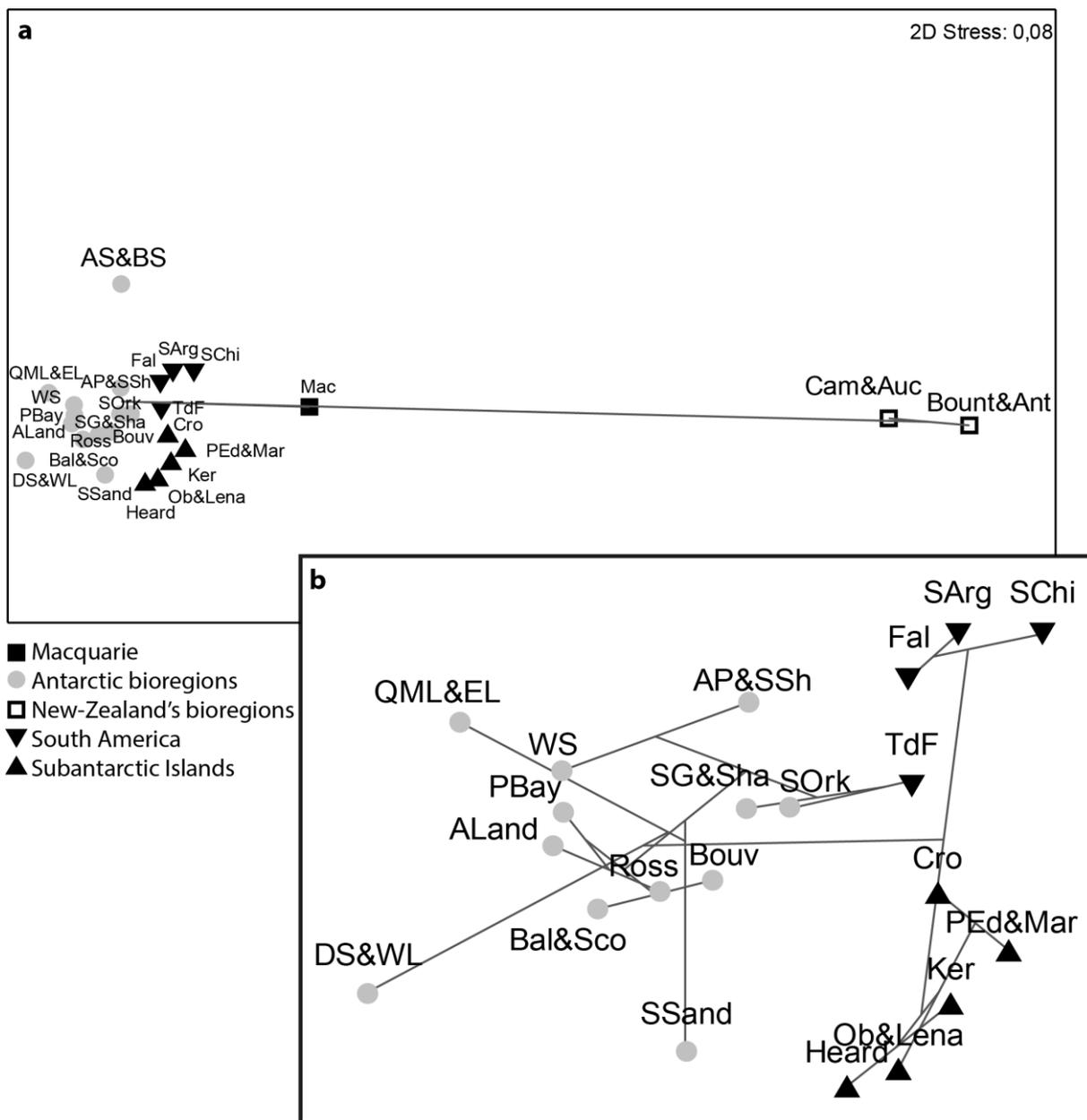


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Figure 3



810 Figure 4



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