

Seaweeds in Two Oceans: Beta-diversity

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2 ABSTRACT

3 Several species assembly mechanisms have been proposed to structure ecological communities. We assess
4 the biogeography of seaweeds along 2,900 km of South Africa's coastline in relation to a thermal gradient
5 produced by the Agulhas Current, and contrast this with the environmental structure created by the Benguela
6 Current. We subdivided the coastline into 'bioregions' to examine the regional patterning. To investigate the
7 assembly mechanisms, we decomposed Sørensen's β -diversity into 'turnover' (β_{sim}) and 'nestedness-resultant'
8 (β_{sne}) dissimilarities, and used distance-based redundancy analysis (db-RDA) to relate them to the Euclidian
9 thermal difference, d_E , and geographical distance. Moran's eigenvector maps (MEM) were used as an additional
10 set of spatial constraints. Variation partitioning was then used to find the relative strengths of thermal and
11 spatially-structured thermal drivers. Spatial and environmental predictors explained 97.9% of the total variation
12 in β_{sim} and the thermal gradient accounted for 84.2% of this combined pool. β_{sim} was the major component
13 of overall β -diversity in the Agulhas Current region, suggesting niche influences (environmental sorting) as
14 dominant assembly process there. The much weaker thermal gradient in the Benguela Current-influenced region
15 resulted in a high amount of β_{sne} that could indicate neutral assembly processes. The intensification of upwelling
16 during the mid-Pliocene 4.6–3.2 Ma (i.e. historical factors) were likely responsible for setting up the strong
17 disjunction between the species-poor west coast and species-rich south and east coast floras, and this separation
18 continues to maintain two systems of community structuring mechanisms in the Atlantic and Indian Ocean
19 influenced sides of South Africa.

20 Keywords: beta-diversity, species assembly, seaweed, macroalgae, turnover, nestedness-resultant, Benguela Current,
21 South Africa

22 1 Introduction

23 The assembly processes that structure biodiversity across a range of scales form the theme of macroecology
24 (Chave, 2013). This paper deals with the composition of seaweed assemblages along the ~2,900 km South
25 African coastline, including the identification, description and explanation for the spatially-structured
26 patterns at scales from 100s to 1,000s of kilometers. Inshore conditions along this coastline range from
27 cool through warm temperate to fringe tropical (Bolton and Anderson, 2004; Bolton et al., 2004), and are
28 influenced by two major ocean currents in two oceans that set up a strong thermal gradient along the shore.

29 A gradient in seaweed community composition is hypothesised to arise in response to this temperature
30 gradient (Qian and Ricklefs, 2007), and that deterministic, niche-based species assembly processes will
31 operate in the region.

32 Biodiversity may be described in terms of α -, γ - and β -diversity, with the former two referring to 'local'
33 and 'regional' diversity, respectively. β -diversity as defined by Whittaker (1960, 1972) is a measure of
34 variation in species composition from place to place and is comprised of two processes (Baselga, 2012):
35 the replacement of species independently of the difference in species richness (called 'turnover', β_{sim}) and
36 a term that considers this difference in species richness called ('nestedness-resultant', β_{sne}). The relative
37 contribution of these two processes is not immediately evident from species dissimilarities, and yet such
38 considerations should be implicit in macroecological studies. The ability to decompose β -diversity into
39 turnover and nestedness-resultant components has become possible within the last decade (Baselga, 2010),
40 but the use of this form of β -diversity partitioning has not yet widely permeated the phycological literature
41 (or even in marine studies more broadly; Anderson et al., 2013). Cognisance of spatial scaling should also
42 be deeply rooted in the study of biodiversity more generally, but such questions have only recently begun
43 to be addressed (Barton et al., 2013).

44 Since studies of β -diversity consider the variation in species assembly processes from place to place, and
45 necessitate an understanding of mechanisms that drive these processes (Davidar et al. 2007), studying β -
46 diversity of adjacent coastal marine bioregions or marine provinces (Spalding et al., 2007) could provide
47 deeper insight into how such processes operate along gradients (Qian and Ricklefs, 2007). Few studies
48 dealing specifically with β -diversity exist for marine biota, especially over spatial areas in excess of 1,000s
49 of kilometers. Recent examples include studies on fish distribution (Zintzen et al., 2011; Anderson et al.,
50 2013), the biogeography of macroalgae along 6,600 km of Australian coastline (Leaper et al., 2011),
51 and a study on deep-sea bivalves (McClain et al., 2011). All four have β -diversity as a primary interest.
52 However, macroecological studies in the terrestrial realm, such as along mountain slopes or across latitudes,
53 have yielded the most comprehensive insights into the drivers responsible for assembling species into
54 communities (Whittaker, 1960; Davidar et al., 2007; Qian and Ricklefs, 2007; Soininen et al., 2007). What
55 these studies show is that, perhaps universally, high rates of species turnover are associated with steep
56 environmental gradients. Species turnover is of practical importance to spatial biodiversity planning.
57 Focusing conservation efforts on areas of high β -diversity will ensure the preservation of a diversity of
58 species and their environmental niches. Peaks in β -diversity along ecoclines may indicate boundaries
59 between bioregions, highlighting regions where communities are poised at their environmental limits, thus
60 aligning with long-term monitoring surveys that aim to project ecosystem responses to climatic change.

61 The controlling effect of seawater temperature on the survival and reproduction of benthic organisms and
62 patterns in the evolution and ecology of biological assemblages at regional scales is well known (van den
63 Hoek, 1982b; Breeman, 1988; Blanchet et al., 2008; Broitman et al., 2008; Byrne et al., 2009; Verbruggen
64 et al., 2009; Wieters et al., 2009; Couce et al., 2012; Potts et al., 2014). It influences the species composition
65 of the biota associated with various thermal zones, which forms patterns on global, regional and local
66 scales (Tittensor et al., 2010; Spalding et al., 2012). At the global scale, ocean currents and latitudinal solar
67 heat flux gradients maintain the ocean's thermal regime. At local scales (<10 km) at the land/sea margin,
68 additional physical phenomena contribute to thermal patterns that may differ markedly from those at the
69 mesoscale (*i.e.* spatial scales >50 km), and which are observable through remote sensing. Consequently,
70 the different properties of the temperature regime which set up the biogeographical patterns are less well
71 known, especially at regional and local scales near the land where satellite data poorly reflect reality (Smit
72 et al., 2013). Most studies that recognise temperature as a major driver of species distribution take the

73 annual mean temperature (Tittensor et al., 2010); fewer recognise the importance of variability and range
74 (e.g. Couce et al., 2012; Tyberghein et al., 2012). Detailed laboratory culture studies with seaweed species,
75 for example, closely link biogeographical distribution limits with maximum and minimum monthly mean
76 temperatures (van den Hoek, 1982b; Breeman, 1988). The time-integrated ‘thermal environment’ is an
77 amalgam of various statistical properties derived from a multitude of instantaneous temperature recordings,
78 and it is relevant to question if one or a few of these properties have an overriding imprint on the species
79 assembly.

80 Using a detailed data set of seaweed presence and absence coupled with coastal seawater temperature
81 climatologies, we investigated the thermal properties and species composition of 58 coastal sections spaced
82 around the South African coastline. The coastline is broadly influenced by two major ocean currents, the
83 Benguela Current and the Agulhas Current. One is an eastern boundary upwelling system and defines a
84 cool temperate environment, and the other a western boundary current driving meridional transport of
85 sub-tropical water towards the tip of Africa. We were primarily interested in establishing how these ocean
86 currents, of which the effect at the coast can readily be measured as gradients in thermal properties, may
87 have influenced the species assembly processes operating along an approximately 2,900 km long coastline.
88 To do so, we first link matrices of species dissimilarity to environmental distance matrices and Moran’s
89 eigenvector maps (MEM) using distance-based redundancy analysis, and then apply variance partitioning
90 (Peres-Neto and Legendre, 2010) to determine the relative contributions of thermal metrics and other
91 spatially-organised drivers of seaweed community composition (as seen in the β -diversity components,
92 β_{sim} and β_{sne}). Second, we examine how the thermal and spatial structuring agents operate at smaller spatial
93 scales within marine provinces of the region by undertaking a more detailed analysis of the various distance
94 matrices, and also ask which of the thermal properties we examined were most influential in setting up
95 the patterns that emerged. Our findings are congruent with existing knowledge (e.g. Stephenson, 1948;
96 Lom, ???; Spalding et al., 2007) and add a more nuanced understanding of the processes responsible for
97 structuring the seaweed biodiversity in the sub-region.

98 2 Methods

99 2.1 Species data and explanatory variables

100 We used three sets of data in this analysis. The first comprises distribution records (presence/absence) of
101 846 macroalgal species belonging to the Divisions Ochrophyta, Rhodophyta and Chlorophyta within each
102 of 58 \times 50 km-long sections of the South African coast (mentioned in **bold** font in the text and listed in
103 Appendix A, Table1). The *seaweed data* represent ca. 90% of the known seaweed flora of South Africa,
104 but excludes some very small and/or very rare species for which data are insufficient. The data are from
105 verifiable literature sources and our own collections, assembled from information collected by teams of
106 phycologists over three decades (Bolton and Stegenga, 2002; Bolton, 1996, 1986; De Clerck et al., 2005;
107 Stegenga et al., 1997).

108 The second is a dataset of *in situ* coastal seawater temperatures (Smit et al., 2013) derived from daily
109 measurements over up to 40 years. The *thermal data* set was used as the first set of explanatory variables. The
110 following statistical properties were entered into the analysis: the means for the year (*annMean*), February
111 (*febMean*, Austral summer) and August (*augMean*, Austral winter); the annual standard deviation (SD)
112 around the mean for the year, February and August (*annSD*, *febSD* and *augSD*, respectively); and the annual
113 thermal range between the mean temperature of the warmest and coldest months (*annRange*), and the
114 mean range of February and August temperatures (*febRange* and *augRange*).

The third set of explanatory variables was generated to represent the spatial connectivity among coastal sections. Because of the strong environmental gradients along the shore, species community composition should be spatially organised (including the modelled spatially structured environmental variables, exogenous spatial variables and autocorrelation), and this was accounted for in the analysis. To this end we produced a section–section connectivity matrix based on a minimum spanning tree (MST) topology, starting from a geographical distance matrix. This topology focuses on relationships between neighbouring sections and discards connections that are further away. In the case of the coastline data, sections are connected only to other sections that are below a certain truncation distance. This largely resulted in a ‘string-of-beads’ series of section–section connections; for example, Section 4 is directly connected to only Sections 3 and 5; sections at the termini of the coastal ‘string’ of sections are each connected to only one other section. We generated Moran’s eigenvector maps (MEM; Dray et al., 2006, 2012) from this connectivity matrix through a principal coordinates analysis (PCoA) using the PCNM function of the PCNM package in R 3.3.3 (R Core Team, 2017), and kept the MEMs with positive spatial correlation. The MEMs are completely orthogonal and represent the spatial structures over the full range of scales from 50 to 2,900 km. Large eigenvectors represent broad spatial scales while smaller ones cover finer features. The *spatial data* were used as the second set of explanatory variables in multiple regression type analyses (Dray et al., 2012). Details and code are provided in Appendix B.

2.2 Distance-based redundancy analysis and variance partitioning

Using the distance-based redundancy analysis (db-RDA; Minchin, 1987) implemented with the capscale function of the R package, vegan (Oksanen et al., 2016), we explored the role of the thermal and spatial descriptors in structuring the seaweed communities across the 58 coastal sections. To represent the biotic data, we decomposed Sørensen’s dissimilarity ($\beta_{\text{sør}}$) into its ‘nestedness-resultant’ (β_{sne}) and ‘turnover’ (β_{sim}) components (Baselga, 2010) using the betapart package (Baselga et al., 2013). This approach was necessary because β -diversity is strongly coupled with α -diversity, and it allowed us to make inferences about the possible drivers of β -diversity. Turnover refers to processes that cause communities to differ due to species being lost and/or gained from section to section, *i.e.* the species composition changes between sections without corresponding changes in α -diversity. The nestedness-resultant component implies processes that cause species to be gained or lost, and the community with the lowest α -diversity is a subset of the richer community.

The assessment of the biotic ordination within the context of the underlying environmental properties proceeded using the environmental variables’ z -scores. To determine the descriptors that best describe the patterns in the seaweed dissimilarity data, we first applied full (global) db-RDAs using the complete sets of thermal and spatial variables, separately for each set. Using the forward selection procedure implemented in the packfor package for R (Blanchet et al., 2008), we reduced the number of variables in each set and retained only those that best fit the biotic data. Forward selection prevents the inflation of the overall type I error and reduces the number of explanatory variables used in the final model, which improves parsimony. The reduced set of thermal variables retained collinear variables (Graham, 2003), which were identified and removed using variance inflation factors (VIF; Dormann et al., 2013). This was not necessary for the MEMs as they are orthogonal by definition. The remaining significant orthogonal thermal and spatial variables were then regressed with β_{sim} and β_{sne} and final db-RDA models produced. The computation of db-RDAs was followed by permutation tests of the adjusted R^2 to assess the significance of constraints (thermal and spatial descriptors). Lastly we undertook variance partitioning (Peres-Neto et al., 2006; Peres-Neto and Legendre, 2010) between the environmental (thermal) and spatial predictors using the varpart function in

158 the **vegan** package. Refer to Appendix B for more information about the methodology and for the R code
159 underlying the analysis.

160 **2.3 Analyses of dissimilarity and distance matrices**

161 We then explored regional patterns in β -diversity. Because connectivity between sections is constrained by
162 their location along the shore and thus direct distances between sections do not apply, the total distance
163 between a pair of arbitrary sections is the cumulative sum of the great circle distances between each
164 consecutive pair of intervening sections along the coast (this is in fact encapsulated by the connectivity
165 matrix used in the PCNM analysis, above). Plots showing the relationship of β_{sim} and β_{sne} with distance
166 are limited because they do not provide a geographical context. To overcome this problem, we used a
167 ‘network graph’ to show spatial relationships in regional species dissimilarity. See Appendix C for details
168 and R code.

169 The last step of our analysis was applied to the four bioregions recognised for South Africa (Bolton and
170 Anderson, 2004), namely the Benguela Marine Province (BMP; 1–17), the Benguela-Agulhas Transition
171 Zone (B-ATZ; 18–22), the Agulhas Marine Province (AMP; 19–43/44) and the East Coast Transition Zone
172 (ECTZ; 44/45–58). To this end, we calculated an Euclidian distance matrix that encapsulated all pairwise
173 differences between coastal sections for each of the thermal metrics highlighted in the db-RDA (above)
174 using the **vegan** package; these are called thermal differences (d_E) throughout. We then correlated β_{sim}
175 and β_{sne} with geographical distance and d_E and provided matching plots in which the four bioregions were
176 colour-coded to discern bioregional affiliations and differences. Together these analyses were able to capture
177 β -diversity at two spatial scales: among sections within bioregions, and among all sections for the whole
178 country.

179 **3 Results**

180 **3.1 The thermal environment and species richness**

181 South Africa’s annual mean coastal water temperature ranged from $12.0 \pm 0.9^\circ\text{C}$ (mean \pm SD) at its north-
182 western limit near the Namibian border (1) to $24.0 \pm 1.9^\circ\text{C}$ on the east coast near the Mozambican border
183 (58) (Fig. 1). The global latitudinal gradient of diminishing temperature with increasing latitude was seen
184 only along the east coast where the annual mean temperature decreased from ca. 24.5°C near 58 to 17.5°C
185 around 39. The alongshore thermal gradient for this 950 km stretch of coastline was ca. 0.7°C per 100 km,
186 with steeper gradients near 54. The latitudinal gradient largely reversed in direction along the west coast
187 (1–16), i.e. temperatures became slightly cooler further north.

188 **Figure 1 near here.**

189 On average, these data indicated an increase in inshore annual mean temperatures from west to east
190 (1–58) of $12.1\text{--}24.4^\circ\text{C}$ (range: 12.3°C). In February the thermal range was 13.7°C , while in August it was
191 10.5°C . In August the west–east temperature transition was smooth whereas in February substantial warm
192 fluctuations in the mean monthly temperature were observed in embayments such as 13 and the False Bay
193 sections from 17–18, and 28 and some sections around 35/36 and Algoa Bay from 34–36. In summer the
194 mean monthly temperature gradient steepened between 19–28, and thereafter decreased eastwards along
195 the coast from 33–34.

196 The number of species within the BMP was low, and many northern sections had fewer than 150 species,
197 and it rose significantly in the warmer section around 12/13, and the southern sections around the Cape
198 Peninsula (16/17). Thereafter, richness increased markedly in the B-ATZ, the AMP and the ECTZ. The
199 highest number of species in any one section was 340 (Section 39 near the eastern end of the AMP).

200 3.2 Environmental correlates of seaweed diversity

201 db-RDA, forward selection and the assessment of VIF retained *augMean*, *febRange*, *febSD* and *augSD* as
202 the most parsimonious descriptors of β_{sim} with an adjusted R^2 of 0.885, explaining 89.8% of the variation
203 (global permutation test on final model: d.f. = 4, $F = 110.16$, $p = 0.001$). The model consisted of two
204 significant canonical axes: CAP1 and CAP2 explained 73.3% and 14.9% of the variation, respectively. The
205 biplot scores (vectors) showed that *augMean* was heavily loaded along CAP1 and the metrics related to
206 variation around the mean, *i.e.* *febRange* and *febSD*, strongly influenced β_{sim} along CAP2 (Fig. 2). Plots
207 of the 'lc' scores on geographic axes are given in Fig. 3. The scores representing CAP1 increased gradually
208 along the shore from west to east, reflecting the pervasive influence of *augMean* as coastal sections changed
209 from cool to warm temperate through to sub-tropical thermal regimes. CAP2 site scores were lowest along
210 the southern sections. β_{sne} was only influenced by *annMean* (Fig. 2) along CAP1 that explained 20.3% of
211 the total variation ($R^2 = -0.140$, d.f. = 1, $F = -6.018$).

212 Figure 2 near here.

213 The db-RDA analysis procedure retained 17 significant MEMs that fully encapsulated the spatial
214 dependence within β_{sim} (d.f. = 18, $F = 84.055$, $p = 0.001$), resulting in an adjusted R^2 of 0.963 and accounting
215 for all of the variation. Fifteen canonical axes were produced of which five were significant. The first one
216 alone explained 77.1% of variance with the remaining axes accounting for *ca.* 1% or less of the inertia.
217 MEM2, MEM3 and MEM5 were most strongly loaded along CAP1 (Fig. 3). These MEMs caused the
218 sections belonging with the BMP to separate out from all other sections, and also for the northern sites
219 of the ECTZ to diverge from the sections and bioregions further south. The scales of spatial dependence
220 captured by these MEMs could all be considered to be broad-scaled. Two canonical axes comprised of two
221 significant MEMs were able to explain 87.3% of the variation in β_{sne} (R^2 of 0.437, d.f. = 4, $F = 12.06$, $p =$
222 0.001; Fig. 3). CAP1 consumed 79.0% of the inertia due to MEM1 and MEM5.

223 Figure 3 near here.

224 The partitioning of the variance associated with the seaweed community along the coast (Table 1) was
225 explained jointly by the thermal and spatial variables selected in the preceding db-RDAs. Combining
226 the thermal and spatial predictors (fractions [E+S]) allowed the model to capture 97.9% of the total β_{sim}
227 variance ($F = 191.56$, $p = 0.001$), with a residual variance of 2.1%. The thermal variables on their own
228 (*i.e.* those that are spatially unstructured; fraction [E|S]) were able to account for only 1.8% of the total
229 variation ($F = 20.506$, $p = 0.001$), but including some spatially structured thermal properties, [E], raised
230 the proportion of explained variation to 84.2% ($F = 110.16$, $p = 0.001$). Pure spatial patterning (*i.e.* in the
231 absence of temperature influences, perhaps with exogenous environmental influences or autocorrelation;
232 fraction [S|E]) drove 13.7% of the species variation ($F = 23.649$, $p = 0.001$), and adding some thermal
233 influences together with spatial descriptors, [S], increased this to 96.1% ($F = 80.731$, $p = 0.001$). Turning
234 now to β_{sne} , we see that our explanatory variables were less successful in capturing the variation. The spatial
235 variables, [S], and the spatial plus thermal variables, [E+S], were able to account for 67.8% ($F = 12.06$, $p =$
236 0.001) and 71.4% ($F = 9.077$, $p = 0.001$) of the variation, respectively.

237 Table 1 near here.

238 3.3 Pairwise dissimilarities

239 Network graphs show the spatial relationships of β_{sim} (Fig. 4). β_{sim} clearly highlighted the effect of the sharp
 240 change in α -diversity between the BMP and the B-ATZ. Sections in the B-ATZ retained similarities with
 241 sections as far east as 33 within the AMP. Eastwards from 30 similarities with sections within the ECTZ
 242 became apparent, but they generally did not extend past 43. Aside from a very low similarity with sections
 243 at the eastern extent of the AMP, the ECTZ sections retained similarities with sections within the same
 244 biogeographical province only over very short distances, and again it highlighted the high β -diversity in
 245 this region.

246 **Figure 4 near here.**

247 The overall and regional mean values for the three measures of pairwise β -diversity are presented in Table
 248 2. The overall Sørensen β -diversity ($\beta_{\text{sør}}$, 0.496 ± 0.287) was larger than that of the bioregions, and only a
 249 small fraction of it was comprised of nestedness-resultant β -diversity. Of the four bioregions, the ECTZ
 250 had the highest $\beta_{\text{sør}}$ (0.259 ± 0.157). At the bioregional scale, it is important to note that the nestedness-
 251 resultant component was about four times larger for the BMP ($\beta_{\text{sne}}/\beta_{\text{sør}} = 0.581$) than that of the other three
 252 ($\beta_{\text{sne}}/\beta_{\text{sør}}$ ranged from 0.097 to 0.170).

253 Plots of β_{sim} and β_{sne} among all possible section pairs indicated clear differences among the four
 254 bioregions in their relationships with geographic and thermal distances (Fig. 5). The BMP showed a
 255 weak relationship between β_{sim} and distance ($r^2 = 0.052$; regression statistics in Table 3) since much of
 256 the compositional variation between sections in this region was due as much to nestedness-resultant β -
 257 diversity as it was to turnover (Fig. 5) as noted above (see $\beta_{\text{sne}}/\beta_{\text{sør}}$ in Table 2). Within the ECTZ (~900
 258 km long coastline) and the B-ATZ (only 170 km long) the rates were moderate at $\beta = 0.079$ ($r^2 = 0.936$)
 259 and high at $\beta = 0.109$ ($r^2 = 0.658$) per 100 km, respectively. In the AMP it was lower at $\beta = 0.029$
 260 per 100 km ($r^2 = 0.834$). Higher rates (β) indicate that communities turned over more rapidly per unit
 261 distance of coastline; furthermore, this also provided strong evidence that β -diversity was structured along
 262 environmental gradients. β -diversity was less influenced by changes in species numbers between sections
 263 in the B-ATZ, AMP and the ECTZ, as these two marine provinces were characterised by a relatively even
 264 number of species and hence had low β -diversities attributed to nestedness (Fig. 5). β_{sim} expressed with
 265 respect to the *augMean* thermal distance showed similarly steep slopes for three of the bioregions (β 's
 266 ranging from 0.290 to 0.350, with $r^2 > 0.605$), with that for the BMP about a two-thirds lower (Fig. 5;
 267 Table 3). With respect to *febRange*, a significant relationship with β_{sim} existed only for the two transitional
 268 areas, the B-ATZ and the ECTZ (r^2 of 0.548 and 0.583, respectively; Fig. 5). The steepness of the relationship
 269 between β_{sim} and the latter thermal metric was lower than that seen with *augMean*. Concerning *febSD*, this
 270 relationship was steepest for the B-ATZ ($\beta = 0.103$, $r^2 = 0.276$) and then the ECTZ ($\beta = 0.082$, $r^2 = 0.310$;
 271 Fig. 5); the same general trend held for *augSD*, with $r^2 = 0.310$ and $r^2 = 0.276$ for the ECTZ and B-ATZ,
 272 respectively. The pattern of β_{sne} with geographic and thermal distance was generally significant but very
 273 poor (low r^2 -values) and with weak gradients (β) (Fig. 5). The notable outcome there was that it was the
 274 BMP where β_{sne} was strongest even though its r^2 values were weak ($r^2 = 0.205$ and 0.164 for the relationship
 275 with geographical distance and thermal distance, respectively).

276 **Figure 5 near here.**

277 **Table 2 near here.**

278 **Table 3 near here.**

279 4 Discussion

280 This study considered the drivers of seaweed β -diversity at the scale of bioregions (marine provinces) nested
281 within a ~2,900 km stretch of coastline. With the exception of some Australian studies (Smale et al.,
282 2010, 2011; Waters et al., 2010; Leaper et al., 2011; Wernberg et al., 2013), one in Europe (Tuya et al., 2012)
283 and another two in the Arabian region (Schils and Wilson, 2006; Issa et al., 2016), studies of this scale and
284 nature have so far been infrequently seen for marine macroalgae. Of the above-mentioned studies, only two
285 specifically considered β -diversity (Leaper et al., 2011; Issa et al., 2016). Our data focus on the taxonomic
286 representivity of a region by aggregating species occurrence records within 50 km long sections of coastline,
287 and are blind to the effects of small-scale habitat heterogeneity (e.g. as seen in Smale et al., 2010). For this
288 reason we cannot infer influences of stochastic processes and other aspects of environmental heterogeneity
289 at scales of <50 km. Rather, our data emphasise broad biogeographic patterns (Lawton, 1999) with induced
290 spatial dependence (Peres-Neto and Legendre, 2010) emerging as the main species assembly process east of
291 the Cape Peninsula. This points to deterministic niche influences that correlate with environmental drivers
292 at broad spatial scales. These environmental and biotic patterns reflect the nature of the two dominant
293 ocean currents of the region, and we see that β -diversity at the scale of the country is moderately high and
294 generally influenced by processes that cause species turnover (β_{sim}). Environmental drivers are comprised
295 mostly of thermal properties of seawater with a strong spatial dependence across a broad scale (82.4%) and a
296 smaller amount of unknown non-thermal broad-scale spatial influences (13.7%). Only in the species-poor
297 west coast region is there evidence of neutral assembly processes (e.g. dispersal limitation, and stochastic
298 processes as one might expect within kelp forests), as shown by the higher rates of nestedness-resultant
299 β -diversity (β_{sne}) emerging there.

300 The most comprehensive assessment of global marine biogeography (Spalding et al., 2007) places much
301 of South Africa's coast within two realms: Temperate Southern Africa (from southern Angola to around
302 56°S) and the western-most edge of the Western Indo-Pacific Realm (across the Western Indian Ocean to
303 Sumatra). The transition into the Western Indian Ocean realm is just visible in Section 57 where our data
304 show a steady rise to tropical water temperatures that exceed 20°C, between 28.5 and 29°S. Our study region
305 is too restricted to capture the rates of β -diversity change at the transition of realms. Here we would expect
306 higher rates of turnover than we report for the smaller-scale 'Provinces' and transition zones that make up
307 the Temperate Southern African Realm (see below). We would also expect this at higher taxonomic levels,
308 consistent with the definition for a realm (Spalding et al., 2007): this is true for the temperate Southern
309 African seaweed floras, which have high species endemism but very low generic endemism (except for the
310 Fucales, Ochrophyta). We hypothesise that this is because the cool temperate region may be geologically
311 recent (4.6–3.2 Ma, Marlow et al., 2000).

312 Nested within the realms are marine provinces, areas that according to (Spalding et al., 2007) are large,
313 with distinct biotas, some level of endemism (mainly at species level), and distinctive abiotic environments.
314 In this context, the Benguela and Agulhas Currents prescribe the broadest scale hydrographic features
315 whose imprint can be seen, at that scale, on the seaweed flora: they maintain the Benguela Marine Province
316 (BMP) and Agulhas Marine Province (AMP, as per Spalding et al., 2007) of South Africa, separated
317 by an area of transition. The southward flowing Agulhas Current has an overriding effect on the east
318 coast, extending as far as the eastern portion of the Western Cape Province (58–22). Along the east
319 coast it is responsible for setting up a region that transitions from sub-tropical in the north to warm
320 temperate near Cwebe (i.e. the region 58–44), which is termed the East Coast Transition Zone (ECTZ).
321 From 44–22 the Agulhas Current continues to maintain an influence on the coast, but its direct effect is
322 subdued because of the widening of the continental shelf southwards of Cwebe, and the warm-temperate

323 biogeographical region, the AMP, is consequentially formed. The northward flowing Benguela Current
324 from which upwelling is maintained by prevailing south-easterly trade winds influences the remainder of
325 the Western Cape Province (west of 22), particularly from the western side of the Cape Peninsula (16/17)
326 northwards to about 16°S. The influence of the Benguela Current here defines a cool-temperate regime, the
327 BMP, with the range of monthly mean temperatures at most sections intermediate between cold-temperate
328 and warm-temperate, according to the definitions of (Lüning et al., 1990).

329 The oceanographic features of the Benguela and Agulhas Currents set up gradients in seawater
330 temperature that run predominantly from east to west (*i.e.* August mean temperatures increasing in this
331 direction), but also from north to south (*i.e.* with the southern coastline becoming more variable in its
332 thermal regime). Of particular ecological importance is the gradient in August mean temperature. It clearly
333 structures the thermal distance decay curve, which shows a steadily increasing dissimilarity in thermal
334 distance along the shore from 1. The gradient may be smooth or punctuated at irregular intervals by
335 peaks in dissimilarity. Specifically, the mean temperature for Austral winter (August) increases more-or-
336 less smoothly from the west. Within the region, species richness along the coastline reflects the general
337 global trend — for most taxa but ironically not for seaweeds (Bolton, 1994; Santelices et al., 2009) — of
338 diminishing diversity with decreasing temperature, which at that scale is seen as a latitudinal gradient:
339 the cold temperate area of the west coast has a much lower α -diversity than the warm temperate and sub-
340 tropical south and east coasts, with the latter two regions having similar values. This same pattern exists
341 for fish and invertebrates in this region, albeit in data which include coastal waters further from the shore
342 (Griffiths et al., 2010). In the previous presentation of the seaweed dataset (Bolton and Stegenga, 2002), the
343 ECTZ had far fewer species per section than the AMP, but this change in the dataset results from significant
344 research in the period 2000–2005 on the seaweeds of the ECTZ (De Clerck et al., 2005). In contrast, bringing
345 the annual mean temperature or thermal range during Austral summer into the calculation of the thermal
346 distance introduces several large punctuations in dissimilarities between some sections — most notably
347 near Cape Point into False Bay (17), and near 30 and 48. The region of the coastline where low biodiversity
348 community composition changes to highly biodiverse communities is reflected in the β -diversity, which
349 peaks around the Cape Peninsula (16/17). Correlations between β -diversity (resulting from a change in
350 α -diversity) and areas of transition have also been noted in several studies on terrestrial biota (Melo et al.,
351 2009; Tonial et al., 2012), but such investigations are less established for marine biota (Schils and Wilson,
352 2006; Anderson et al., 2013).

353 β -diversity is generally lower within individual bioregions than at the scale of the country, because the
354 coastlines are shorter and large differences in diversity cannot approach that which can occur over the entire
355 coastline. Even within bioregions, β -diversity is still *generally* dominated by species turnover rather than
356 by nestedness-resultant processes. The exception is the BMP where nestedness-resultant (β_{sne}) assembly
357 processes contribute to around 58% of the β -diversity. The generally strong influence of turnover-based
358 processes elsewhere highlights the role of environmental drivers, which here are spatially structured as
359 one would expect of the steep environmental gradients, and hence of niche influences (*i.e.* environmental
360 filtering) in determining species assembly (Fitzpatrick et al., 2013).

361 It seems plausible that factors linked with the establishment of oceanographic regimes (historical
362 factors *sensu* Baselga et al., 2012) that influenced dispersal and speciation along the coast resulted in
363 the current-day gradients in β -diversity within bioregions. This hypothesis was put forward to explain
364 the low endemism and low species richness of Ochrophyta in the upwelling dominated west coast of
365 southern Africa (Bolton, 1986). But is the underlying mechanism the selection of cold tolerant species
366 from amongst a more diverse pool in the wider region (Bolton, 1986), or is it due to a dispersal barrier

that prevented elements of the warmer south coast seaweed flora from occupying the west coast? Evidence from seaweed phylogeography postulates different evolutionary origins for seaweeds of the BMP and AMP (Hommersand, 1986; Hommersand and Fredericq, 2003). The mechanism could be the intensification of upwelling during the mid-Pliocene 4.6–3.2 Ma (Marlow et al., 2000). Turnover is almost entirely absent in favour of nestedness-resultant processes in the BMP, but the AMP is defined entirely by a moderate rate of turnover with respect to both geographical and thermal distance. The dominance of the nestedness-resultant component of β -diversity within the BMP suggests that the complex, non-linear influence of the annual mean temperature selectively influences species richness from section to section in a pattern that is not spatially coherent, but this climatic variable (*i.e.* fraction [E], which has *some* spatial structure) explains only 39.1% of the β_{sne} patterning in the region. Unaccounted-for non-climatic variables and perhaps non-environmental variables may explain some of the remaining variation. This points to habitat and/or environmental heterogeneity and neutral processes such as dispersal limitation, stochastic influences or habitat heterogeneity as the main structuring agents of communities within the region. Indeed, habitat heterogeneity generated through stochastic influences such as patchiness due to storms denuding portions of kelp beds (which is the dominant habitat type along the west coast) is well-known in kelp forests (Smale et al., 2011). Furthermore, the prevalence of two kinds of assembly processes to either side of the Cape Peninsula (17), coinciding with the point where a region of low α -diversity (BMP) transitions into a region of higher α -diversity (the Benguela-Agulhas Transition Zone, B-ATZ), suggests that the answer to our question is probably that some historical event was responsible for that disjunction, and that this barrier is still maintained today due to limited mixing between the Agulhas and Benguela Currents (although some of the sections along the west coast between 16/17 and 10 certainly have a reasonable probability of sharing species with sections at the western-most side of the AMP, *e.g.* 23, 24; see more on the B-ATZ, below).

Rapid rates of species turnover with respect to geographic and thermal distance along the east coast, and the steep decrease in species richness around the 16/17–22 transition region, suggest that relatively more endemic species should occur within the BMP and AMP. Seawater becomes warmer along a steep gradient along the east coast northward towards 54 where-after there is a further steepening of the gradient towards Mozambique (north of 58). This steepening of the already strong temperature gradient in the northern portion of the ECTZ supports the conclusion of (Bolton and Anderson, 2004) that it represents the transition from a tropical Indian Ocean seaweed flora in Mozambique to a temperate flora in the south. A similar pattern exists for the rocky intertidal biota in the region (Sink et al., 2005). The temperature of the coldest month of the year sufficiently accounts for the environmental gradient in all bioregions, except for in the BMP. This strong coupling between the thermal gradient and β_{sim} suggests that a niche difference mechanism is the primary species compositional assembly process (Nekola et al., 1999). This implies species being sorted based on their physiological tolerances along a gradient, and the particularly high rate of species turnover along the east coast reflects the species' narrow thermal ranges. Species here have narrow local distributions, and there is only a 2% seaweed endemism in the region (Bolton and Anderson, 2004).

The overlap region between 22 and the southern tip of the Cape Peninsula (16/17), which we call the B-ATZ, is an area where aspects of both currents may be periodically seen (Largier et al., 1992), and it is not surprising that biogeographically this region includes biotic elements from the marine provinces on both sides of it. This is clearly visible in our analyses, which show the highest rates of species turnover (β_{sim}) with respect to geographical distance, the mean temperature for August and the range in temperature in February. This is a form of regional biogeographical structuring called the temporal/spatial constraint model (Nekola et al., 1999). Similar conclusions with regards to the B-ATZ being an transitional area have been reached by (Stephenson, 1948; Bolton, 1986; Bolton and Anderson, 2004; Mead et al., 2013). For marine macroalgae at least, this area cannot be recognised as a marine province as it does not meet the

412 criteria for it to be classified as such (Spalding et al., 2007), *i.e.* it lacks cohesion, levels of endemism, and
413 there is an absence of distinct abiotic features (with exception of such conditions periodically arising in
414 False Bay due to prevailing mesoscale oceanographic conditions).

415 It was recently suggested that studies which associate marine macroalgal distributional patterns with
416 broad-scale temperature gradients neglect to consider alternative or additional explanations, such as that
417 offered by connectivity due to ocean currents (Wernberg et al., 2013). It is possible that seaweeds are
418 similarly influenced by ocean currents around South Africa, and it is tempting to suggest that the *direction*
419 of turnover along the east coast is from north to south, and along the south coast from east to west, as this
420 would coincide with the direction of the Agulhas Current. From a purely thermal point of view, the imprints
421 of those ocean currents are certainly present at the coast in the zone that our seaweed data represent, but
422 the physical processes that operate in that coastal zone are considerably more complex and decoupled from
423 mesoscale influences (Schlegel et al., 2017). Personal observations by one of us (AS) recount dislodged
424 individuals of the kelp, *Ecklonia maxima*, having washed ashore some 400 km east of the eastern-most
425 distributional limit for the species in South Africa — this is *against* the direction of the current, which
426 in this region is situated considerably far from the shore along the edge of the Agulhas Bank. Our data
427 on the rate of species turnover as a function of the thermal difference between coastal sections (β_{sim}
428 *vs.* d_E) within bioregions show an almost precise relationship between thermal difference and change in
429 species composition (even though the relationship between d_E and geographical distance differs between
430 the east and south coasts), and provide very strong support for temperature, rather than connectivity due
431 to currents, as an overriding driver of seaweed community composition over large spatial scales. Within
432 the context of Beijerinck's 'Law' that "everything is everywhere but the environment selects" (De Wit and
433 Bouvier, 2006), the only role that ocean currents can have in setting up biogeographical patterns is to
434 cause *everything not to be everywhere*. At these scales, with or without the influence of ocean currents,
435 temperature still selects. In other words, at broad spatial scales within the region encompassed by the
436 ECTZ and the AMP, the seaweed flora is structured predominantly by niche-assembly processes driven
437 by a thermal gradient.

438 However, we should point out that *ca.* 13.7% of the seaweed flora's turnover is also explained by
439 some other broad scale spatial influences (MEM2, MEM3 and MEM5), which represent exogenous
440 (unmeasured) environmental variables and autocorrelation. The importance of these relative to each other
441 is unknown. Future work may find that some of these environmental influences may indeed be that of
442 ocean currents, which operate at those broad scales, but our current interpretation does not support this
443 notion. Rather, we suggest that the unknown influence is more likely to be neutral influences (Hubbell,
444 2001) manifesting at a reasonably broad scale. These may include stochastic events (*e.g.* Smale et al., 2011)
445 or biotic processes caused by differences in species demography, dispersal or the influence of grazers, etc.
446 Such processes are usually finer scaled, but, having said that, the entire west coast region that makes up
447 the BMP is dominated by nestedness-resultant β -diversity, which is also symptomatic of neutral assembly
448 processes.

449 4.1 Conclusions

450 Our approach throughout this paper hinges upon the biogeographical provinces and overlap regions
451 defined using both seaweed and thermal data. Together, thermal and species gradients/patterns provide
452 the most parsimonious explanation for the processes assembling the seaweed flora within the study region.
453 The explanation is that thermal gradients set up β -diversity based on species turnover as a result of
454 environmental filtering within the southern and eastern coastal sections, while along the west coast a

455 very different kind of assembly process, nestedness-resultant β -diversity, emerges. We suggest that this
456 disjunction results from a historical event that is currently still limiting connectivity between the Indian
457 and Atlantic Oceans around the Cape Peninsula.

458 We also show how thermal metrics other than the annual mean temperatures can aid in the delineation
459 of macroecological patterns. Some species are limited by cold and some by warm temperatures, and
460 the constraining factor may differ at a species' southern and northern limits (e.g. van den Hoek, 1982a;
461 Breeman, 1988). If these are important determinants, as we indeed show there are, other measures of
462 climate should be used in our repertoire of explanatory variables. For example, the mean temperature for
463 the coldest month, standard deviation, variation in annual temperature extremes, or temperature ranges
464 (e.g. as used by Qian and Ricklefs, 2007; Leaper et al., 2011) may readily be extracted from time series of
465 daily temperatures. These approaches, as we apply them here, may greatly improve macroecological and
466 biogeographic studies and aid our ability to analyse broad-scale communities patterns and the processes
467 that assemble them.

468 **Conflict of Interest Statement**

469 The authors declare that the research was conducted in the absence of any commercial or financial
470 relationships that could be construed as a potential conflict of interest.

471 **Author Contributions**

472 AS conceptualised the scope of the research reported in this paper, undertook all the numerical and
473 statistical analyses, made the first round of interpretation, and did the bulk of the writing. JB and RA
474 collected all the samples over the last 30 years, compiled the database of species distribution records for the
475 region included in this analysis, contributed in equal part to the conceptualisation of the research and the
476 interpretation of the findings, and provided significant editorial input into penultimate and final drafts of
477 the document.

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486 **References**

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Tables

Table 1. Variance partitioning of β_{sim} and β_{sne} by the thermal and spatial predictors. F and p -values are shown for the testable fractions only.

Fraction	d.f.	Adj. r^2	F	P
turnover, β_{sim}				
[E], thermal variables	4	0.842	110.160	0.001
[S], spatial variables	16	0.961	80.731	0.001
[E+S], all thermal and spatial	20	0.979	191.560	0.001
[E S], thermal, non-spatial	4	0.018	20.506	0.001
[E with S], spatially structured thermal		0.824		
[S E], spatial, non-thermal	16	0.137	23.649	0.001
1-[E+S], residual variance		0.021		
nestedness-resultant, β_{sne}				
[E], thermal variables	1	0.391	-6.017	—
[S], spatial variables	4	0.678	12.060	0.001
[E+S], all thermal and spatial	5	0.714	9.077	0.001
[E S], thermal, non-spatial	1	0.040	-1.018	0.997
[E with S], spatially structured thermal		0.355		
[S E], spatial, non-thermal	4	0.323	14.277	0.001
1-[E+S], residual variance		0.286		

Table 2. β -diversity (β_{sor}) as well as its partitioning into β_{sim} and β_{sne} components. The partitioning represents the contribution of turnover and nestedness-resultant processes. Mean \pm SD values are presented for the whole South African coast, as well as for each of the four bioregions.

Region	β_{sor}	β_{sim}	β_{sne}	$\beta_{\text{sne}}/\beta_{\text{sor}}$
BMP	0.105 ± 0.086	0.044 ± 0.053	0.061 ± 0.059	0.581
B-ATZ	0.098 ± 0.068	0.083 ± 0.071	0.014 ± 0.009	0.143
AMP	0.117 ± 0.076	0.087 ± 0.067	0.030 ± 0.020	0.170
ECTZ	0.259 ± 0.157	0.234 ± 0.162	0.025 ± 0.018	0.097
overall	0.496 ± 0.287	0.433 ± 0.277	0.063 ± 0.061	0.127

Table 3. Linear regressions of pairwise β_{sim} and β_{sne} as a function of the geographical or thermal distance between the section pairs. The thermal distances that best explain β_{sim} and β_{sne} were selected during the db-RDA procedure. Here, β is the slope of the regression line (per 100 km in the case of the relationship with distance), and the P -value test the hypothesis that the slope is significantly different from 0 using a t -test. Refer to Fig. 5a–g.

bioregion	β	t -value	P	Adj. r^2
β_{sim} vs. distance				
BMP	0.007 ± 0.002	3.886	<0.001	0.052
B-ATZ	0.109 ± 0.016	6.873	<0.001	0.658
AMP	0.029 ± 0.001	44.751	<0.001	0.834
ECTZ	0.079 ± 0.001	65.003	<0.001	0.936
β_{sim} vs. augMean d_E				
BMP	0.009 ± 0.012	0.765	0.445	-0.001
B-ATZ	0.342 ± 0.060	6.139	<0.001	0.605
AMP	0.290 ± 0.010	29.209	<0.001	0.681
ECTZ	0.350 ± 0.011	31.200	<0.001	0.772
β_{sim} vs. febRange d_E				
BMP	0.008 ± 0.011	0.710	0.479	-0.002
B-ATZ	0.259 ± 0.047	5.491	<0.001	0.548
AMP	-0.006 ± 0.004	-1.422	0.156	0.003
ECTZ	0.183 ± 0.009	20.102	<0.001	0.583
β_{sim} vs. febSD d_E				
BMP	0.018 ± 0.011	1.583	0.115	0.006
B-ATZ	0.161 ± 0.080	2.029	0.054	0.115
AMP	-0.007 ± 0.002	-2.758	0.006	0.016
ECTZ	0.171 ± 0.013	13.401	<0.001	0.383
β_{sim} vs. augSD d_E				
BMP	0.038 ± 0.008	4.590	<0.001	0.073
B-ATZ	0.103 ± 0.032	3.183	0.004	0.276
AMP	-0.003 ± 0.003	-0.936	0.350	0.000
ECTZ	0.082 ± 0.008	11.411	<0.001	0.310
β_{sne} vs. distance				
BMP	0.015 ± 0.002	8.178	<0.001	0.205
B-ATZ	0.006 ± 0.004	1.541	0.137	0.054
AMP	0.006 ± 0.000	15.255	<0.001	0.367
ECTZ	-0.001 ± 0.001	-2.200	0.029	0.013
β_{sne} vs. annMean d_E				
BMP	0.067 ± 0.009	7.141	<0.001	0.164
B-ATZ	0.037 ± 0.013	2.929	0.008	0.240
AMP	-0.009 ± 0.004	-2.499	0.013	0.013
ECTZ	-0.002 ± 0.003	-0.845	0.399	-0.001

Figures and captions

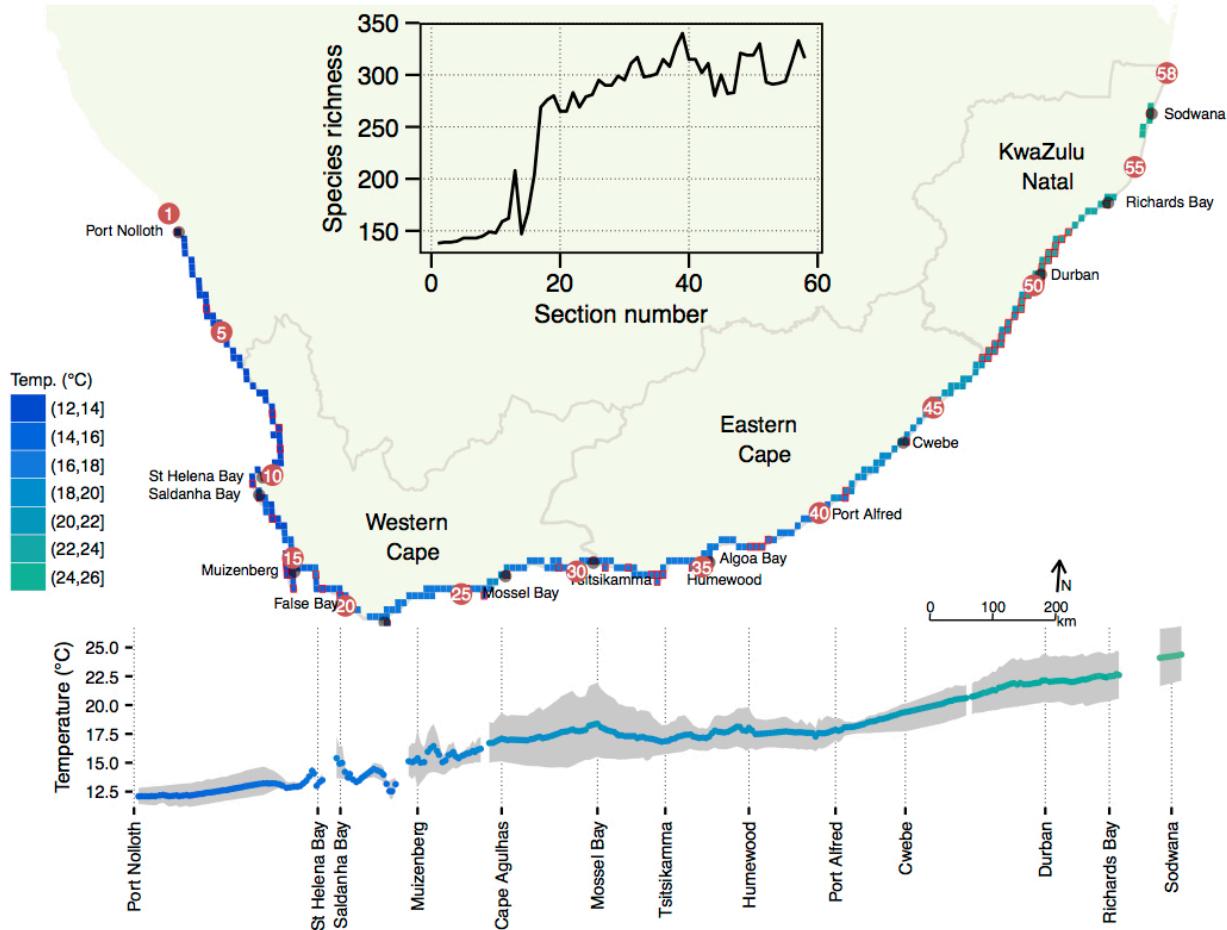


Figure 1. Profile of mean annual temperature along the coast of South Africa. Profiles are indicated as a function of geographical position on a coastal map (top) and as a function of distance away from Section 1 (bottom). The latter visualisation also indicates the long-term minimum (mean August) and maximum (mean February) temperatures as a grey shaded area around the annual mean temperature. The inset shows the species richness of macroalgae along the coast. Note that although a detailed temperature profile is displayed here, further analyses in this paper proceed with temperature data interpolated to the 58 sections for which seaweed diversity data are available.

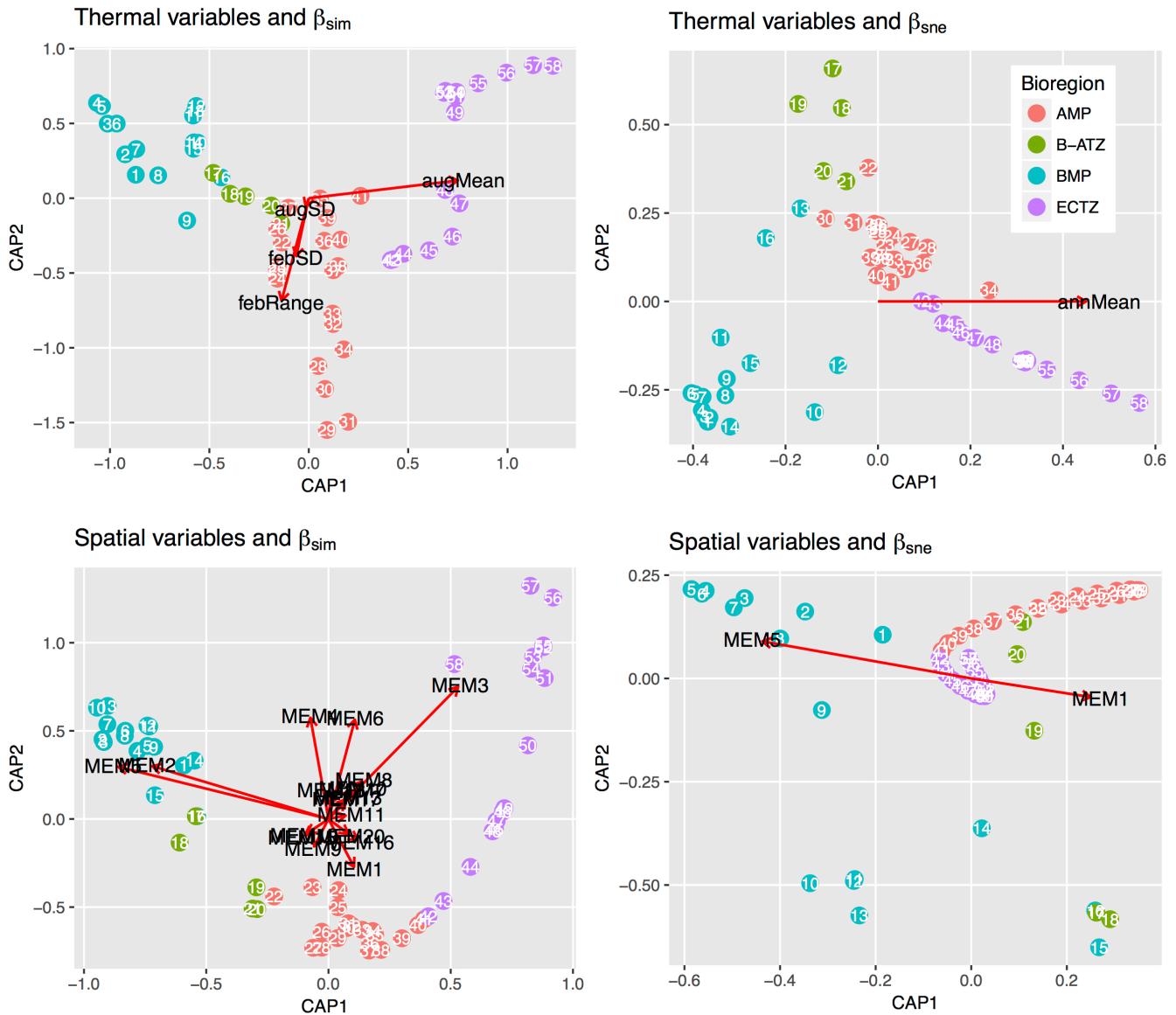


Figure 2. db-RDA biplots of tc scores for β_{sim} and β_{sne} constrained by the thermal and spatial MEM variables. The only two canonical axes shown are CAP1 and CAP2 since these capture the bulk of the inertia present in the ordinations. The constraining vectors were selected during the db-RDA steps.

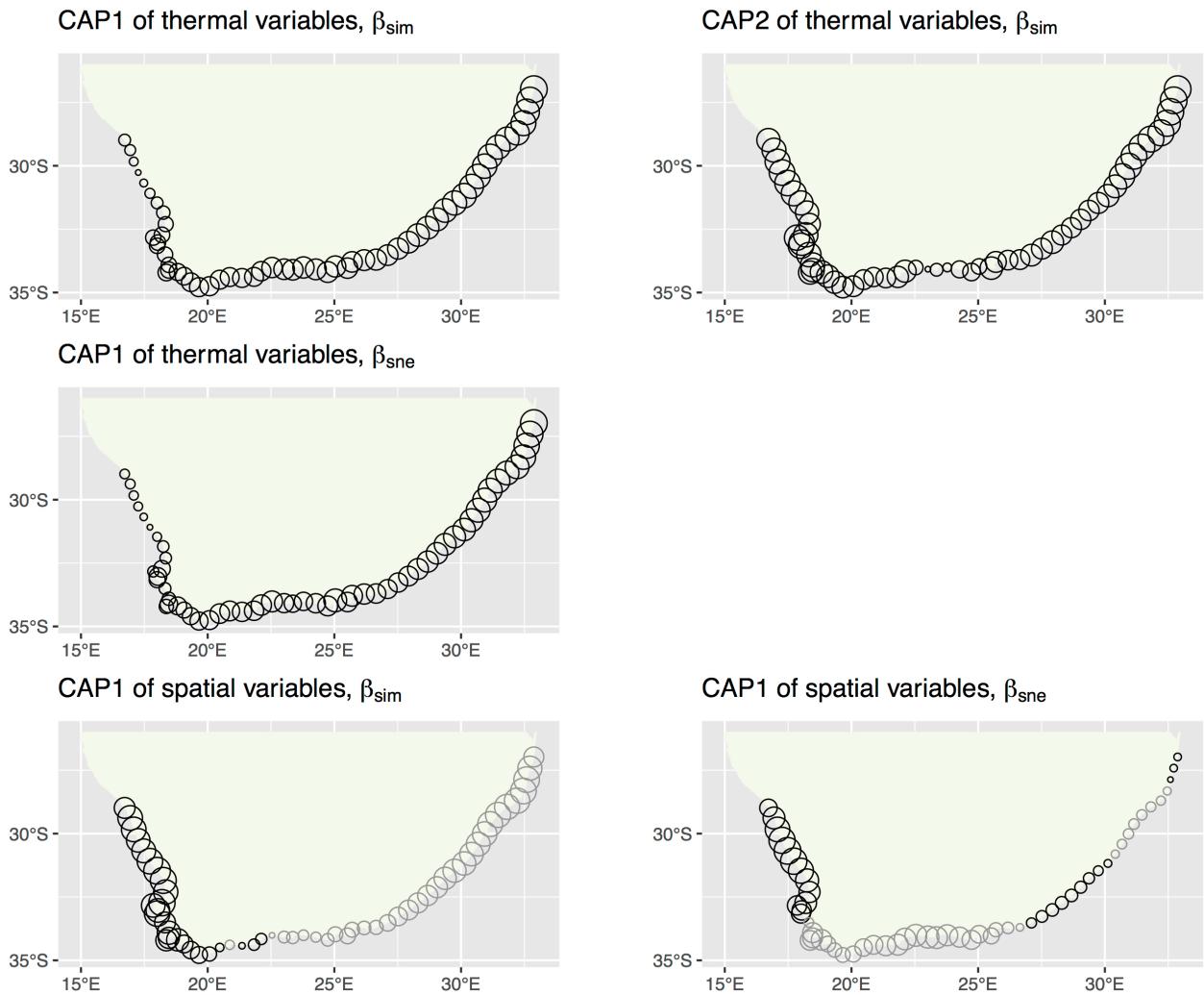


Figure 3. db-RDA site scores for β_{sim} and β_{sne} on geographic coordinates. The site scores indicate the major gradients captured by the environmental and spatial (MEM) constraints. Gray circles indicate negative site scores.

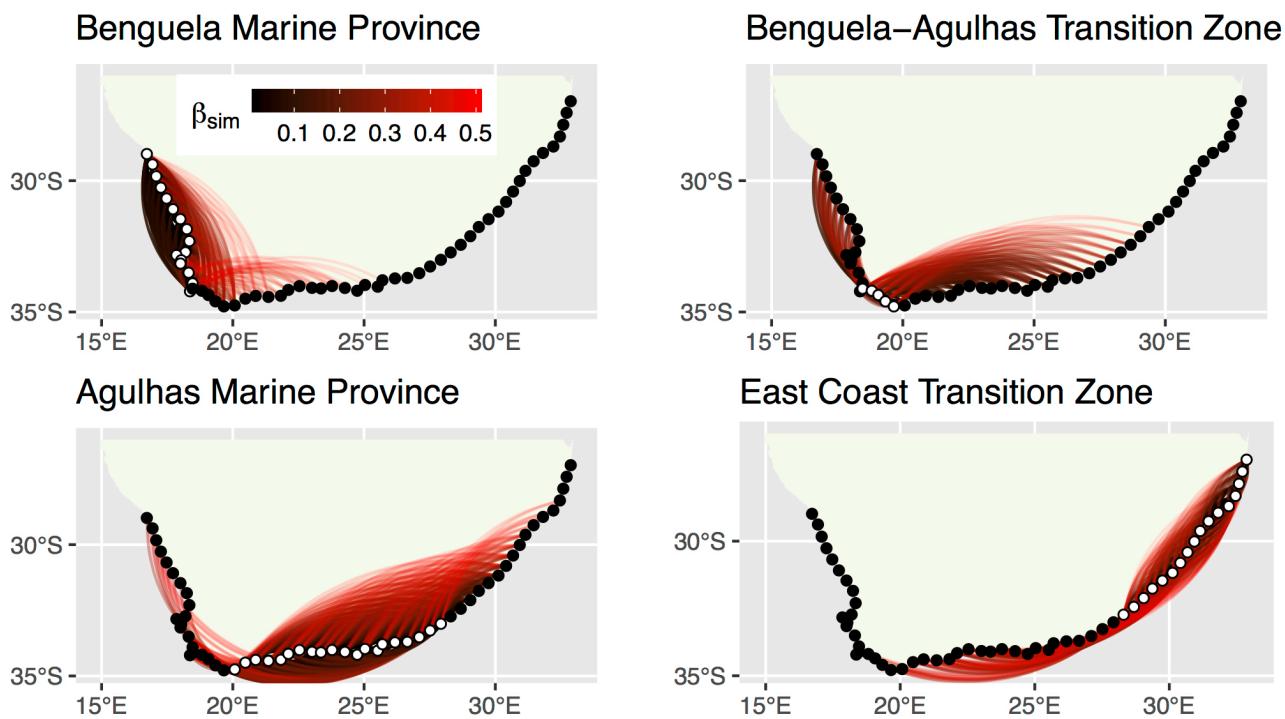


Figure 4. Network graphs of pairwise β_{sim} showing sections that are similar to one-another in species composition. Dissimilarity indices range from >0.0–0.5 (possible dissimilarities range from 0.0–1.0). The 58 sections in Appendix A appear as dots at the vertices of the network graph, with those belonging with the ‘active’ bioregion shown in white. The pairwise dissimilarities are shown by the coloured lines, with blacker lines indicating lower dissimilarity indices (species composition more similar) and redder ones higher dissimilarity indices (species composition more dissimilar).

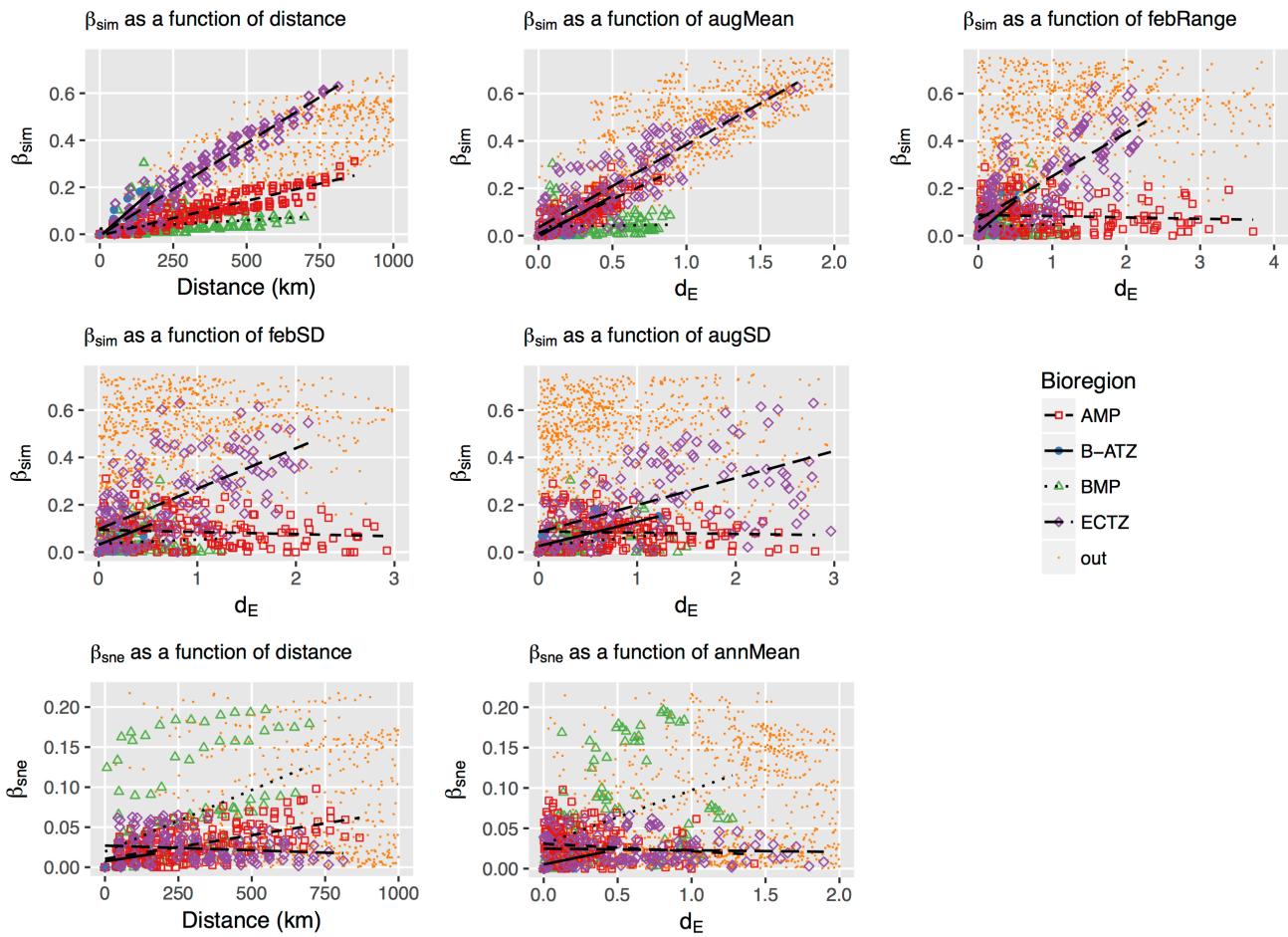


Figure 5. Plots of the turnover (β_{sim}) and nestedness-resultant (β_{sne}) forms of β -diversity as a function of geographical or thermal distance between the coastal sections. The influential d_E variables (*augMean*, *febRange*, *febSD* and *augSD* for β_{sim} , and *annMean* for β_{sne}) were determined in the db-RDA procedure. β_{sim} , β_{sne} , d_E and geographical distance were calculated as differences between coastal section pairs, and data points representing section pairs falling between bioregions are coloured yellow and labelled 'out'. The strengths and gradients of the regression lines indicated in the panels are presented in Table 3.