RESEARCH ARTICLE

Comparative phylogeography in a marine biodiversity hotspot provides novel insights into evolutionary processes across the Atlantic-Indian Ocean transition

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Abstract

Aim: Intraspecific genetic variation is a key component of biodiversity, with higher diversity indicating greater resilience and population substructuring suggesting unique evolutionary histories. Comparative approaches, in which intraspecific genetic variation is assessed across multiple species, are powerful tools to identify evolutionary hotspots, but are still rarely applied at spatial scales relevant to conservation planning. Here, we use comparative phylogeography to understand patterns and potential drivers of genetic variation within a biodiversity and ocean warming hotspot.

Location: The South African coastline, Indian/Atlantic Oceans.

Methods: A literature search was conducted to obtain mitochondrial DNA cytochrome oxidase *c* subunit I and cytochrome *b* sequence data for 17 marine fish and invertebrate species. From these data, we compared averages of haplotype and nucleotide diversity, and within-region Φ_{ST} between four biogeographic provinces in the region. Mixed linear models tested whether environmental variability, habitat preference, or geographic location significantly influence genetic variation.

Results: Average diversity values differed between haplotype and nucleotide diversity, but both broadly displayed highest diversity levels within the South-West bioregion, which is also a region of high levels of within-region Φ_{ST}. Range in sea surface temperatures (SSTs) was the only significant fixed-effect term in the haplotype diversity mixed linear models. Mean SST, stability in SSTs since the Mid-Holocene and position within the species' geographic distribution all had no significant effect on genetic variation.

Main conclusions: Along this coastline characterized by high environmental heterogeneity, we find that variation in temperature is a prominent source of intraspecific variation. Genetic diversity differs between bioregions, but does not display higher levels within the core of each species' range when assessed across multiple species. With elevated levels of genetic diversity, the South-West region of the South African coast is highlighted as a conservation priority area, representing both high genetic diversity and differentiation across taxa.

Alicia Dalongeville and Erica Nielsen contributed equally.

1 | INTRODUCTION

With increasing human pressures and climate change, ecosystems worldwide face rapid modifications of environmental conditions resulting in biodiversity erosion (Ceballos et al., 2017; Panetta et al., 2018), with knock-on effects on human well-being (Mora et al., 2013). Representation and long-term persistence of biodiversity are central to conservation (Margules & Pressey, 2000; Moilanen et al., 2009), but such goals can only be achieved if organisms are able to respond to global changes with geographic range shifts, acclimatization or adaptation (Chevin et al., 2010). As such, conservation plans need to account for the processes shaping biological variability and species' adaptive potential, from ecosystems to genes (Nielsen et al., 2021; Wagner & Fortin, 2013; Webster et al., 2017). As humanity enters the UN Decade of Ocean Science for Sustainable Development (2021–2030), the importance of monitoring and maintaining genetic diversity within species to protect the adaptive capacity, community function and resilience within populations is widely acknowledged (Nielsen, Henriques, et al., 2021; Thomson et al., 2021), although not necessarily fully accounted for at both national and international scales (Hillebrand et al., 2020). Intraspecific genetic diversity provides the basis for evolutionary processes that enable species to adapt to environmental changes (DeWoody et al., 2021; Schindler et al., 2015), and at the community level, genetic diversity has been positively associated with productivity, functioning and stability in various marine systems (DuBois et al., 2021; Phair et al., 2020; Raffard et al., 2019; Salo & Gustafsson, 2016; Sjöqvist & Kremp, 2016).

Genetic diversity is impacted by effective population size (Kimura, 1985), and influenced by both species characteristics, such as dispersal (Ryman et al., 2014), reproductive strategies (Nunney, 1993) and historical demographic variations (Frankham, 1995), as well as landscape features (Selkoe et al., 2016; Wright et al., 2015). The importance of genetic diversity for adaptation and short-term evolutionary potential is widely acknowledged (Hughes et al., 2008; Stange et al., 2021); yet, the key factors shaping genetic diversity remain ambiguous (Hewitt, 2000; Ludt & Rocha, 2015; Teixeira & Huber, 2021; Toms et al., 2014). For example, it has been suggested that biogeography, specifically core vs. edge effects (i.e. the abundant-centre hypothesis; Eckert et al., 2008), and environmental gradients and habitat stability over time (Hewitt, 2000) play critical roles in determining intraspecific genetic diversity. However, the drivers of intraspecific variation across species have largely been tested in isolation, and most of the few studies that compared multiple drivers of genetic diversity did so at spatial scales too large to be informative for conservation (Manel et al., 2020; Nielsen et al., 2021; Wyborn & Evans, 2021). Multi-species comparisons in particular have immense power to detect patterns in the spatio-temporal variation

of genetic diversity at global scales (De Kort et al., 2021), although patterns tend to differ between regions and systems (Gratton et al., 2017; Manel et al., 2020; Miraldo et al., 2016). Inferences from multi-species studies may be limited by various factors including uneven sampling strategies, comparisons across taxa with different marker types or divergent evolutionary dynamics, but are likely to still resolve broad-scale patterns even where some species may have vastly different population genetic patterns (Page & Hughes, 2014; Wright et al., 2015). Yet, despite the potential power of multi-species analyses in shedding light on evolutionary population patterns and processes, several regions globally remain under-represented.

Population structure, as measured by the distribution of genetic variation, has been recorded across many marine species with a broad range of life-history characteristics, including broadcast spawners and direct developers; yet, few concordant genetic clines have been documented across multiple species (Nielsen et al., 2020; Schiebelhut & Dawson, 2018; Stanley et al., 2018; Teske et al., 2011; Wares, 2002; Wright et al., 2015). Identifying multispecies patterns of genetic differentiation is particularly relevant for understanding regional processes that structure populations, and to disentangle the determinants of connectivity and gene flow in the marine environment at larger scales (Kuo & Avise, 2005; Manel et al., 2020). Furthermore, integrating community-level genetic diversity and differentiation into spatial conservation plans and management is central to ensuring the success of long-term conservation objectives (Nielsen et al., 2017; Phair et al., 2021; Thomson et al., 2021; von der Heyden, 2017).

Environmental and habitat characteristics, both contemporary and historical, are known to shape the spatial distribution of genetic diversity and differentiation (De Kort et al., 2021; Manel et al., 2020; Selkoe et al., 2016). In marine ecosystems, the main seascape features shaping spatial genetic patterns are likely ocean currents (which transport gametes and larvae, but which can also create barriers to dispersal) and habitat discontinuities (Pascual et al., 2017; Schunter et al., 2011; Selkoe et al., 2016; Toms et al., 2014). In particular, sea surface temperature (SST), depth and salinity have been identified as common drivers of genetic variation in various marine taxa (Riginos et al., 2016; Selkoe et al., 2016). Furthermore, including historical environmental variation, and identifying areas of stability in the period from the Last Glacial Maximum (LGM) to today, provides additional insights into the role of historical processes in shaping extant patterns of genetic variation (De Kort et al., 2021; Ludt & Rocha, 2015; Nielsen et al., 2021; Nielsen, Henriques, et al., 2021; Phair et al., 2019).

The southern African coastline, spanning the transition between the Atlantic and Indian Ocean biomes, offers an ideal system to study biogeographic hypotheses, as it is divided into several bioregions that are defined by distinct evolutionary histories and

environmental characteristics (Griffiths et al., 2010). These bioregions broadly consist of the cool, nutrient-rich cool-temperate region on the west coast, and the warm, nutrient-poor warm-temperate and sub-tropical regions on the south and east coasts, with a region of overlap between the Atlantic and Indian oceans, along the South-West coast (Figure 1). The South African coastline encompasses a large variety of ecosystems, including rocky and sandy shores, kelp forests, estuaries and coral reefs, as well as contrasting environmental conditions (Branch & Branch, 2018) that drive high levels of coastal marine biodiversity. Four major phylogeographic breaks have been identified, and most coastal species, including organisms with high dispersal capacities, are divided into genetic lineages whose distributional ranges broadly match the bioregions (Figure 1; Teske et al., 2011; Wright et al., 2015), with evidence for temperature and salinity as important drivers of potential local adaptation (Nielsen et al., 2020; Phair et al., 2019; Teske et al., 2021).

In this study, we compiled published data of genetic diversity from mitochondrial DNA (mtDNA) markers into the most comprehensive dataset for coastal marine species in South Africa generated to date to test multi-species patterns of evolutionary diversity. First, we used a biogeographic approach to investigate the spatial distribution of multi-species genetic diversity (haplotype and nucleotide diversity) and differentiation (Φ_{ST}) along the South African coast, and compare the levels of diversity and differentiation between biogeographic regions and species' habitat preferences. Secondly, we used

a seascape genetics approach to test the effect of environmental and biogeographic variables on multi-species genetic diversity and differentiation. We predict that across multiple species, particularly for obligate rocky shore taxa, genetic diversity will be elevated in areas with long-term habitat and temperature stability, particularly around the south-western and southern coastlines (Phair et al., 2019; Toms et al., 2014), which would suggest shared evolutionary dynamics shaping present-day genetic variation. Not only does our work provide novel insights into the evolutionary dynamics of one of the world's most iconic marine systems but it also contributes towards improving protected area networks in the region.

2 | METHODS

2.1 | Genetic data selection

Mitochondrial DNA markers are useful tools to elucidate large-scale patterns on which to build further analyses (Bowen et al., 2014), and are powerful datasets to perform multi-species analyses (Crandall et al., 2019; Nielsen et al., 2017; Selkoe et al., 2014). As mtDNA continues to be the most prevalent genetic marker employed in molecular studies of southern African marine biodiversity, and because it has proven useful to identify even fine-scale drivers of genetic differentiation and diversity (Bowen et al., 2014; Selkoe et al., 2014,
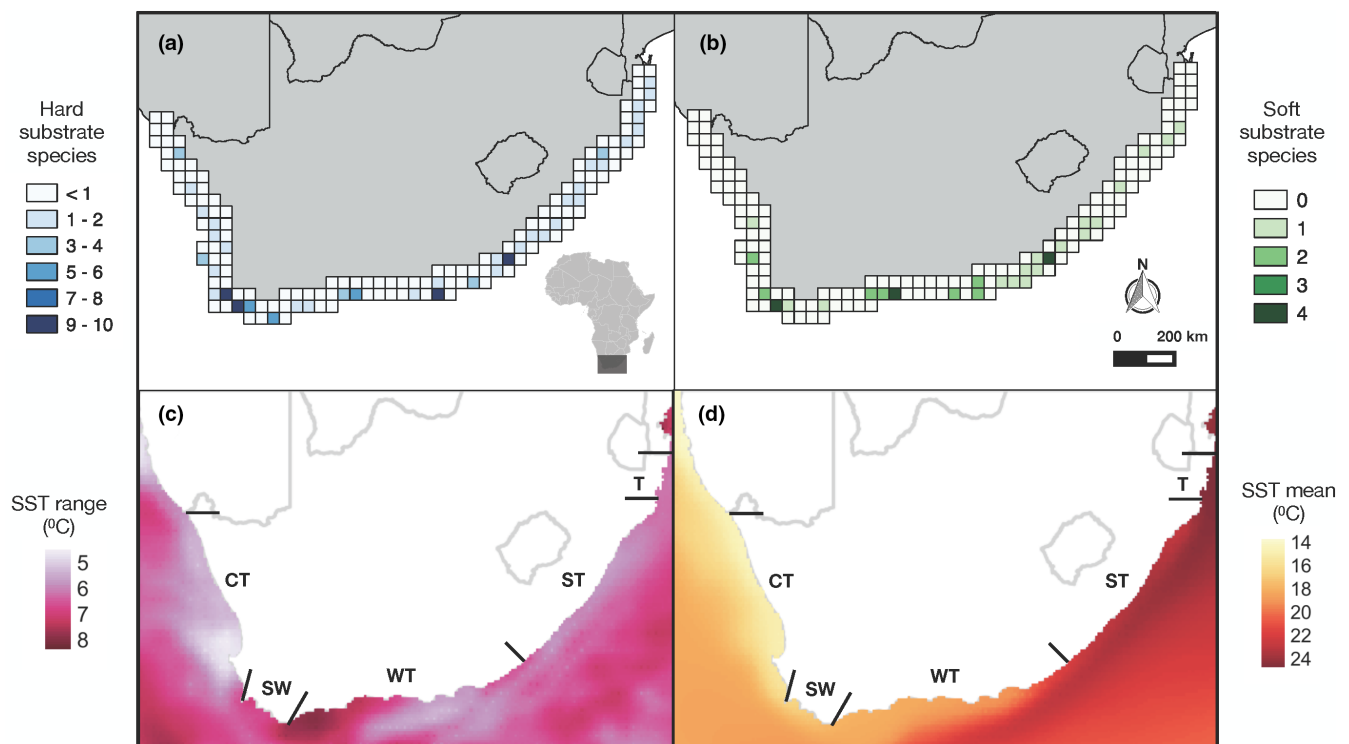
FIGURE 1 The spatial arrangement of the number of species included in the filtered dataset along the coastline, averaged within 30 × 30 km squares, shown for species inhabiting hard substrate (a) habitats and soft substrate (b) habitats. The range in sea surface temperatures (SST; c) and mean SST (d) over 2000–2014 (from Bio-ORACLE database; Tyberghein et al., 2012) is also shown, with the following bioregions overlaid onto the maps (d): Cool Temperate (CT), South-West Coast (SW), Warm Temperate (WT) Sub-Tropical (ST), and Tropical (T)

2016), we compiled mtDNA data of population structure for marine animal taxa in South Africa from the peer-reviewed published literature. We searched the ISI Web of Science using the following terms: South Africa AND ('mtDNA' OR 'mitochondrial') AND ('genetic structure' OR 'genetic differentiation' OR 'genetic diversity') in June 2018. This search returned 678 records, which we further screened to retain only articles that dealt with South African marine animals (i.e. discarding terrestrial and freshwater animals, as well as plant species such as seagrass and algae). Appropriate articles that were not recovered by the Web of Science search were supplemented by the authors' own knowledge of the field in early 2021. We refined the resulting dataset by discarding studies on pelagic species, as they tended to have less consistent sampling and are under different ecological and environmental pressures than coastal species. We also excluded species which are not endemic to southern Africa, i.e. only native South African species were included, as species with global distributions will likely be under different evolutionary constraints than endemic species.

Summarized statistics were collated from compiled studies, in which we recorded published parameters of haplotype diversity (h) and nucleotide diversity (π), along with sample size, and spatial coordinates (longitude and latitude). To account for differences between molecular markers, we chose to only include data from the mtDNA cytochrome b and cytochrome oxidase c subunit I regions. We retained only sites with at least eight individuals sampled per site, from at least nine sites total, with at least two sites per bioregion, to avoid bias due to low sampling size (Hale et al., 2012). We further removed species if they were not sampled in all bioregions within their geographic range (Table 1; Table S1). In addition to measures of diversity, we also categorized species into being associated with hard (predominantly rocky shores) or soft (predominantly sandy systems) substrates.

To assess genetic diversity patterns along the South African coastline, and how they relate to biogeographic patterns, we compared genetic diversity values between predefined biogeographic regions that were based on previously identified bioregions and phylogeographic breaks (Teske et al., 2011): Cool Temperate (CT), South-West Coast (SW), Warm Temperate (WT), Sub-Tropical (ST) and Tropical (T). The tropical bioregion was not included in the analyses, as there was insufficient sampling. Bioregions were included in subsequent analyses if at least five species were sampled within them, with each species needing at least two sample sites within that bioregion.

We also calculated Φ_{ST} values within each bioregion to measure fine-scale population differentiation along the coastline. A different set of species were included in the Φ_{ST} analyses (Table S2), as raw genetic data were needed to calculate within-bioregion genetic variation. The same set of filters as above were applied to the Φ_{ST} analyses, with the additional filter of requiring species to have phylogeographic breaks aligned with biogeographic breaks (so as to not bias within-bioregion Φ_{ST} estimates). We calculated within-region Φ_{ST} with analysis of molecular variance (AMOVA) tests, using Tamura and Nei genetic distances (Excoffier et al., 1992; Tamura &

TABLE 1 Mean h and π per bioregion for each habitat type with number of species and samples (N). The total and average sample sizes are indicated in brackets: N (total number of individuals sampled) and Sites (average number of individuals sampled per site)

Bioregion	Hard substrate habitat					Soft substrate habitat					Total				
	N	Sites	Species	h	π	N	Sites	Species	h	π	N	Sites	Species	h	π
Cool Temperate	25	11	7	0.737 (±0.254)	0.0057 (±0.0055)	4	3	2	0.733 (±0.271)	0.0046 (±0.0057)	29 (1491)	14 (30.0)	9	0.737 (±0.251)	0.0056 (±0.0054)
South West	21	6	8	0.884 (±0.114)	0.0071 (±0.0039)	7	5	3	0.877 (±0.061)	0.0227 (±0.0029)	28 (656)	11 (22.9)	11	0.882 (±0.102)	0.011 (±0.0158)
Warm Temperate	41	9	11	0.818 (±0.229)	0.0064 (±0.0040)	24	15	4	0.804 (±0.143)	0.0156 (±0.0248)	65 (1493)	24 (23.8)	15	0.813 (±0.200)	0.0098 (±0.0158)
Sub-Tropical	38	18	13	0.636 (±0.268)	0.0037 (±0.0036)	15	8	4	0.788 (±0.152)	0.0185 (±0.0354)	53 (966)	26 (19.1)	17	0.679 (±0.250)	0.0079 (±0.0198)
Total	125	44	13	0.758 (±0.248)	0.0056 (±0.0044)	50	31	4	0.804 (±0.15)	0.0166 (±0.0278)					

Nei, 1993). To estimate the degree of structure among groups within a region, we ran AMOVAs including all sample sites per bioregion in Arlequin v.3.5 (Excoffier & Lischer, 2010), using permutation tests with 10,000 permutations to determine significance using a *p*-value of .05.

2.2 | Predictors of genetic variation

We tested the effect of four contemporary and 12 historical climatic predictors expected to influence the spatial genetic patterns of marine organisms (Selkoe et al., 2016) on genetic diversity and differentiation. Including both contemporary and paleo-climatic data was considered appropriate because mitochondrial genetic variation is expected to reflect historical climatic change particularly well compared to more quickly evolving markers, such as microsatellites (Epps & Keyghobadi, 2015). The 16 predictors were obtained from remote sensing at a 5-arc-minute spatial resolution, and downloaded from the Bio-ORACLE platform using the R package 'sdmpredictors' version 0.2.10 (Assis et al., 2018). The following four contemporary climatic variables were obtained over the period 2000–2014 from the Bio-ORACLE database (Tyberghein et al., 2012): mean and range of the annual values of both sea surface temperatures (SST) and sea surface salinities (SSS). The same four variables were also obtained for palaeo-climatic conditions from the MARSPEC database (Sbrocco, 2014) over the Mid-Holocene (6 ka) and the Last Glacial Maximum (21 ka). For each variable, the values per site were extracted from the raster as the average within a buffer of 50 km around a particular site. We calculated climatic stability from either the Mid-Holocene or LGM by taking the absolute difference in mean values of SST or SSS between the present and the time point of interest.

As the position within a species' geographic range is expected to influence intraspecific genetic diversity (de Kort et al., 2021; Nielsen, Henriques, et al., 2021), we also calculated each site's 'range position' as a predictor of genetic variation per species. The centre point of each species' range and the distance from each sample site to the range centre were measured along the coastline with the 'roadgraph' tool in QGIS (Hanson & Seeger, 2017).

2.3 | Statistical analyses

First, *h* and π were log-transformed to achieve normal distributions. We fitted a linear model with genetic diversity (*h* and π) as a response variable, and bioregion or habitat (preferred substrate) as an explanatory variable. We used an analysis of variance (ANOVA) to evaluate the significance of the effect of each explanatory variable on haplotype and nucleotide diversity. We then performed a Dunn's test of multiple comparisons using ranks (Dunn, 1964) implemented in the dunn.test R package version 1.3.5 (Dinno, 2017) to assess the significance of the difference in genetic diversity between bioregions. For representation purposes only, the continuous distribution of *h* and π along the coastline of South Africa were estimated by

conducting an inverse distance-weighted interpolation of the point values for both metrics. The difference in Φ_{ST} between bioregions was assessed using a Kruskal-Wallis, 1952 test for all Φ_{ST} values per bioregion, and then only for significant Φ_{ST} values (*p*-values <.05).

We calculated pairwise Pearson's correlation between environmental predictors (Figure S1). Within each dataset, autocorrelation was removed by eliminating one predictor when Pearson's correlation coefficient was higher than 0.7. A total of 11 variables were removed to account for autocorrelation (see Figure S1), with the final dataset containing four environmental predictor variables: mean sea surface temperature (SSTmean), range in sea surface temperature (SSTrange), mean sea surface salinity (SSSmean), and stability in sea surface temperatures from the present day to the Mid-Holocene (SSTstability_MH), as well as one biogeographic predictor variable: distance from the centre of the species' geographic range (Range_position).

The effect of the environmental predictors on genetic diversity and differentiation was tested using linear mixed models. First, the environmental predictors were standardized using log-transformation. Then, for each genetic diversity response variable (log-transformed *h* or π), we built a full model with all the environmental/biogeographic variables as fixed-effect terms, and bioregion, habitat type and species as random intercept effect terms. For the model including standardized Φ_{ST} as a response, bioregion was not included as a random-effect term since Φ_{ST} values are average measures per bioregion. Instead, the fixed-effect terms were the range in mean SSTs (°C) across each bioregion, as well as the distance along the coast of each bioregion (km), with species as a random effect.

All models were fitted using the function 'lmer' of the lme4 R package version 1.1-18-1 (Bates et al., 2015). To select the most parsimonious models, we performed a backward elimination of random-effect terms followed by backward elimination of fixed-effect terms in the full models. The effect of removing random-effect terms was estimated by likelihood ratio tests, and the effect of removing fixed-effect terms by an *F*-test using Satterthwaite's method for approximating degrees of freedom (Fai & Cornelius, 1996). Model selection was performed using the 'step' function of the R package lmerTest version 3.0-1.9003 (Kuznetsova et al., 2017).

3 | RESULTS

3.1 | Literature review and genetic patterns

The ISI Web of Science search returned 697 articles of which 85 studied genetics of marine organisms. We retained 45 studies that fulfilled the criteria given in the Methods, and selected a final set of data from 13 published articles and one unpublished dataset that used mitochondrial markers (Table S1). After filtering according to the thresholds described in Methods, the final dataset consisted of 175 samples distributed as follows among the four bioregions: 29 samples within the CT region, 28 in SW, 65 in WT and 53 in ST (Figure 1; Table 1). These samples were distributed over 75 sites

along the coastline, with the WT and ST regions having the largest number of sample sites (24 and 26, respectively, Table 1). In addition, there were slightly more sites having species associated with hard (44) compared to soft (31) substrate (Table 1). The final dataset included a total of 17 species: three fishes, ten molluscs, three crustaceans and one echinoderm (Table S1). A total of 4606 individuals were sampled, with a mean sample size of 23.8 individuals per sample (min = 9 and max = 90) across all species and sites (Table S1). Among bioregions, the average sample size ranged from 19.1 to 30.0 (Table 1).

Across the coastline, haplotype diversity ranged from 0.011 to 1 with a mean of 0.765 and a median of 0.85, and nucleotide diversity ranged from 0.0002 to 0.11 with a mean of 0.0082 and a median of 0.0047 (Figures 2, 3; Figure S2). The SW bioregion had the highest average h (0.882 ± 0.102) and highest average π (0.011 ± 0.0158). The ST bioregion had the lowest average h (0.679 ± 0.250) and the CT bioregion had the lowest average π (0.0056 ± 0.0054; Table 1). Bioregion had a significant effect on both h and π, and Dunn's post-hoc test showed that the ST bioregion had significantly different values from those of SW and WT (as shown by the different shapes in Figure 2). While soft substrate species did show higher average diversity values of both h and π than hard substrate species (mean h of 0.804 ± 0.150 and mean π of 0.0166 ± 0.0278 for soft-substrate species; mean h of 0.758 ± 0.248 and mean π of 0.0056 ± 0.0044 for hard-substrate species; Table S1), the effect of substrate type was only significant on nucleotide diversity (Figure 2).

Within-region Φ_{ST} data were calculated for 11 species (Table S2), of which only eight species were retained for analyses after applying the filters of having >eight individuals sampled per site, > two sites sampled per bioregion, and sampled in all bioregions in which the species occurs. Each bioregion passed the additional filters of having >15 sites and >5 species sampled within it. The final dataset consisted of a total of 19 Φ_{ST} measures that were calculated among
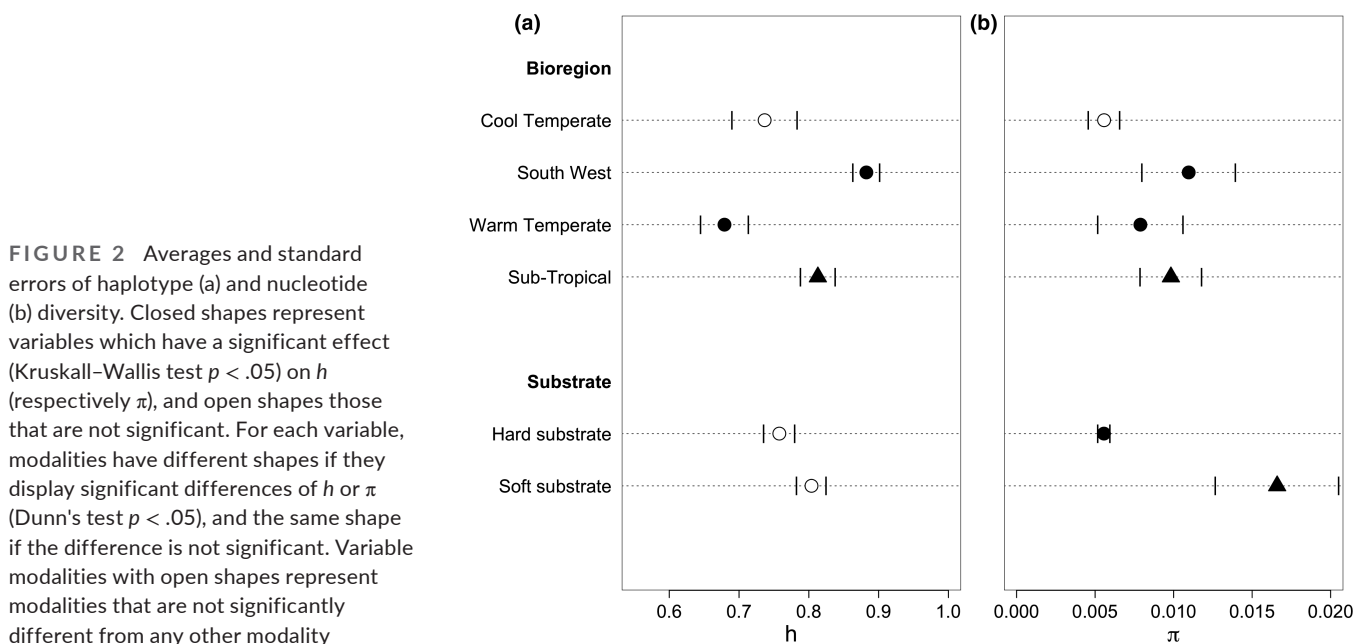
sampled sites within each bioregion, 10 of which were significant ($p < .05$) for five species. For each bioregion, the mean Φ_{ST} and number of species were calculated using all values (Figure 4, in black) and using only significant Φ_{ST} (Figure 4, in grey). The WT bioregion displayed the lowest within-region Φ_{ST} value averaged across species (0.045), whereas the CT bioregion had the highest (0.165).
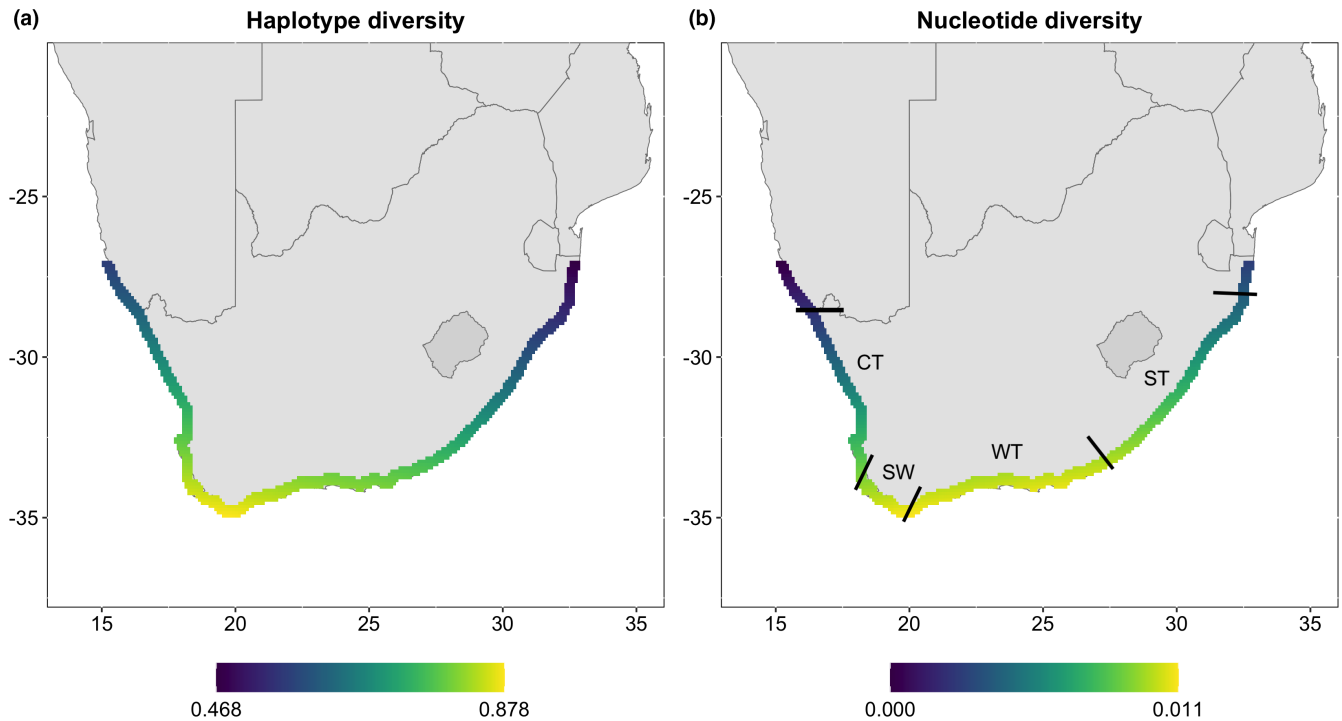
3.2 | Environmental and biogeographic drivers of genetic patterns

Most fixed-effect terms, including range position, mean sea surface salinity and temperature and SST stability since the Mid-Holocene, had no significant effect on either measure of genetic diversity (Table 2). For haplotype diversity, the most parsimonious model included a significant random-effect term for species, and significant fixed-effect terms for range in sea surface temperature (SSTrange). Haplotype diversity was positively correlated with SSTrange (Marginal $R^2 = 0.052$; Figure 5). No significant fixed-effect or random-effect term other than species was found in the π models (Table 2). Within the Φ_{ST} models, the range in mean SST, as well as the length of the bioregion, had no significant effect on the genetic structuring within regions, with the most parsimonious model including only species as a random-effect term (Table 3).

4 | DISCUSSION

Despite South Africa's status as a global marine biodiversity hotspot, the processes driving and maintaining the spatio-temporal patterns of evolutionary diversity of marine species across the Atlantic-Indian Ocean transition zone remain understudied. Using comparative analysis of the most complete dataset of genetic variation of a wide array

FIGURE 2 Averages and standard errors of haplotype (a) and nucleotide (b) diversity. Closed shapes represent variables which have a significant effect (Kruskall–Wallis test $p < .05$) on h (respectively π), and open shapes those that are not significant. For each variable, modalities have different shapes if they display significant differences of h or π (Dunn's test $p < .05$), and the same shape if the difference is not significant. Variable modalities with open shapes represent modalities that are not significantly different from any other modality

FIGURE 3 Heatmaps depicting haplotype (a) and nucleotide (b) diversity along the South African coast. The continuous distribution of haplotype and nucleotide diversity was calculated by conducting an inverse distance-weighted interpolation of the point-values for both metrics

of marine species from South Africa (covering 175 samples from 17 species of fishes, molluscs, crustaceans and echinoderms; Table S1), we investigated the environmental and biogeographic processes shaping coastal biodiversity in the region. We describe multi-species evolutionary hotspots, provide new insights into genetic structuring within bioregions and discuss the environmental variables that are highly correlated with community-level genetic diversity. Our findings not only add significantly to our understanding of the evolution of this important marine biodiversity hotspot but also provide new data relevant for biodiversity conservation in the region.

4.1 | A new state of knowledge of phylogeography for a global marine biodiversity hotspot: From patterns to conservation

The Atlantic-Indian Ocean transition zone has seen a steady increase in the number of population genetic studies, predominantly on single species, calling for critical cross-species inferences on the evolutionary processes shaping spatial genetic diversity in the region. We recovered broadly similar patterns between h and π, which was expected, as they previously have been shown to co-vary (Goodall-Copestake et al., 2012); yet, our results also indicate some discrepancies between the two statistics. For example, π displays higher diversity along the WT region and lower diversity along the CT region compared to h (Figures 2 and 3). These differences could be driven by the fact that haplotype diversity per sample is strictly based on haplotype frequencies, while nucleotide diversity is dominated by

mean sequence divergence (Nei, 1987). Hence, h incorporates population dynamics such as gene flow, making it more variable among samples than π, particularly when sample size is small. Consequently, h may reflect more recent population demographic events, while π displays the influence of older demographic fluctuations. This has important conservation relevance, as these two metrics may potentially lead to the identification of different priority areas if the objective is to protect multiple high diversity areas. The disparity between h and π patterns found here mirrors that found among five coastal species along just the CT region (Nielsen et al., 2017), and suggests that both metrics are needed to fully capture the breadth of genetic diversity when used to inform conservation and management (Beger et al., 2014).

Our results also suggest that mean genetic diversity values (i.e. averaged across sites and species) differ significantly between bioregions, with the ST region being the most distinct (Figure 2). The distinctiveness of that region could be explained by its specific oceanographic characteristics, with a narrow continental shelf and fast-flowing nearshore currents (Branch et al., 2016) and/or by historical factors (Nielsen, Henriques, et al., 2021). The ST region also shows higher levels of phylogenetic and functional diversity than other regions of the South African coast for sparid fishes (Henriques et al., 2020), providing more evidence of its genetic distinctiveness for various marine organisms.

Notably, our analysis of genetic diversity confirms that the SW bioregion, spanning the biogeographic transition zone from Cape Point to the southernmost point in Africa at Cape Agulhas, is a hotspot of evolutionary diversity, characterized by elevated h and
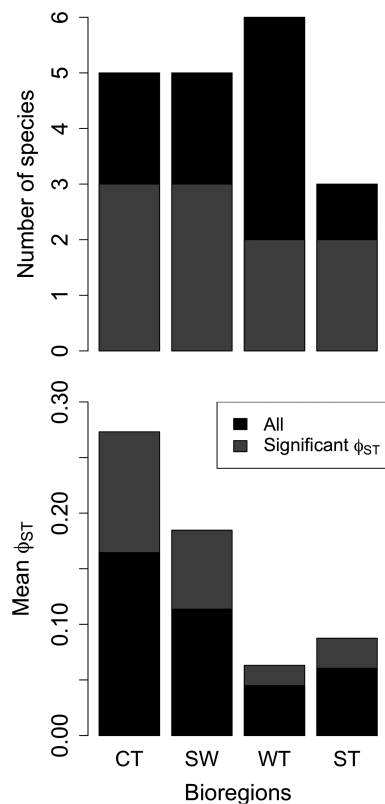
FIGURE 4 Bar chart showing the number of species included in our Φ_{ST} dataset (top) and the mean Φ_{ST} (bottom) for each bioregion. Black bars represent the total number of species (respectively mean Φ_{ST}), and grey bars correspond to the number of species (respectively mean Φ_{ST}) when considering only the significant Φ_{ST} ($p < .05$)

π compared to other areas. This region has also been shown to have increased species diversity, as well as endemicity, of coastal invertebrates (Awad et al., 2002). This is noteworthy because from both a habitat (particularly rocky shore) and temperature perspective, this region seems to have remained relatively stable from the LGM to present and provided a refugial area for marine species in the region. For example, Toms et al. (2014) showed that during the LGM and sea-level lows of up to 120 m, there were significant changes in coastline composition, with much of the present-day rocky shore lost. However, the region around the south-west Cape (as well as a small area further east), has consistent rocky shore habitat, which may well have acted as refugial site for obligate rocky shore species during sea-level fluctuations. Temperature also plays an important role in determining habitat suitability of coastal marine species through time, with both Phair et al. (2019) and Nielsen, Henriques, et al. (2021) showing that the SW bioregion remained suitable for a range of marine species. As refugia have shown to enhance both species richness (Pianka, 1996; Tittensor et al., 2010) and genetic diversity (Hewitt, 2000; Provan & Bennett, 2008; Carnaval et al., 2009), this provides a suitable explanation for the patterns emerging from the SW region. An additional factor could be that some areas of high genetic diversity are likely to be areas of admixture (i.e. where historically distinct evolutionarily significant units overlap; Maggs et al., 2008). Reconstructions of the coastline during the LGM indicate that the topography on the SW coast differed, in that the southern tip of the African continent projected significantly further south (Ramsay & Cooper, 2002), thus potentially providing a barrier between populations to the west and east. Such populations

TABLE 2 Results of the linear mixed models testing the effect of the environmental predictors on genetic diversity. Significant p-values are shown in bold

Predictors	Haplotype diversity			Nucleotide diversity		
	Estimates	**CI**	**p**	**Estimates**	**CI**	**p**
(Intercept)	−1.59	−4.88 – 1.70	.344	.64	−2.34 – 3.61	.675
Range_position	−0.00	−0.00 – 0.00	.616	−0.00	−0.00 – 0.00	.843
SSTmean	−0.00	−0.02 – 0.01	.662	−0.01	−0.02 – 0.00	.232
SSSmean	.05	−0.05 – 0.15	.288	−0.01	−0.10 – 0.08	.773
SSTrange	.07	.02 – 0.11	**.006**	.04	−0.00 – 0.08	.075
SSTstability_MH	−0.00	−0.01 – 0.00	.331	0.00	−0.00 – 0.01	.819
Random Effects						
σ2	0.03			0.02		
τ00	0.05 species			0.03 species		
	0.00 Bioregion			0.00 Bioregion		
	0.00 Habitat			0.00 Habitat		
N	17 species			16 species		
	4 Bioregion			4 Bioregion		
	2 Habitat			2 Habitat		
Observations	162			165		
Marginal R^2 / Conditional R^2	0.153 / NA			0.050 / NA		
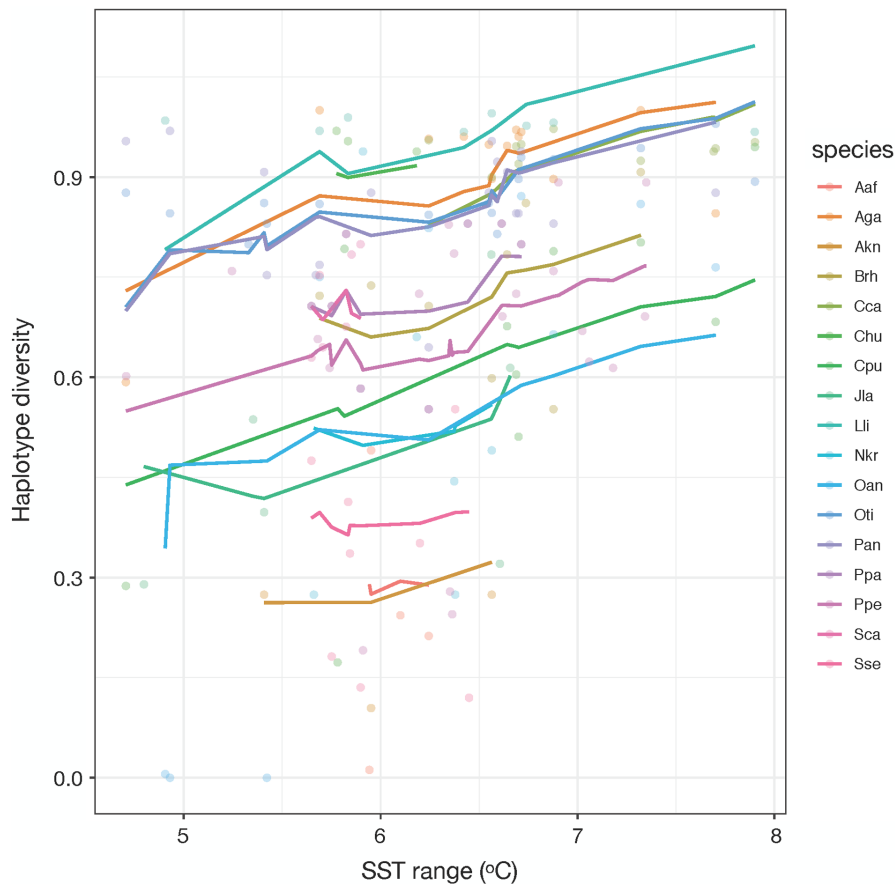
FIGURE 5 Regressions are plotted for the best fitting model, including the relationship between haplotype diversity and the range in contemporary sea surface temperatures (SST range). Lines are coloured to represent regressions for each group of the random-effect term (species; see Table S1 for species abbreviations). As the most parsimonious models for π and Φ_{ST} did not include any fixed-effect terms, the regressions are not shown

TABLE 3 Results of the linear mixed models testing the effect of the environmental predictors on genetic differentiation. Significant *p*-values are shown in bold

Predictors	Φ_{ST}		
	Estimates	CI	*p*
(Intercept)	0.21	−0.74 – 1.16	.638
bioregion_SSTrange	0.46	−0.23 – 1.15	.175
bioregion_distance	−0.15	−0.33 – 0.03	.103
Random Effects			
σ2	0.41		
τ00 species	0.6 5		
ICC	0.61		
Nspecies	8		
Observations	19		
Marginal R^2 / Conditional R^2	0.070 / 0.642		

might now be experiencing admixture through secondary contact (Maggs et al., 2008), hence increasing the genetic diversity in that region, although this pattern does not hold across all species spanning this biogeographic break (Teske et al., 2011; von der Heyden et al., 2008; Wright et al., 2015). From a conservation perspective, our results provide additional evidence for the uniqueness of this area, which is already recognized as the 'Seas of Good Hope' Ecologically and Biologically Significant Area (EBSA) driven by factors such as biological diversity, and highlighting the need for additional management measures that protect both biological and evolutionary diversity within the EBSA.

Interestingly, there were a number of divergent patterns of genetic diversity, supporting the need for further studies describing phylogeographic patterns of marine species. For example, higher levels of haplotype diversity were found in the SW for *Bullia rhodostoma*, *Jasus lalandii*, *Palaemon peringueyi*, and higher levels of nucleotide diversity were found in the same region for *Acanthochiton garnoti*, *J. lalandii* and *Oxystele tigrina* (Figure S3). Some species showed decreasing diversity levels from west to east (*Afrolittorina knysnaensis*, *J. lalandii*, *Parechinus angulosus*, *P. peringueyi* and *Siphonaria serrata*), whereas others showed higher diversity in the ST region (*Afrolittorina africana*, *Nassarius kraussianus* and *Siphonaria*

capensis; Figure S3). Those are typically species with the core distribution along the southern and eastern portion of South Africa's coastline (WT and ST bioregions) and for which the warm-temperate region marks the end of their range and may therefore display lower levels of genetic diversity.

In addition to genetic diversity, we also report the most comprehensive review on genetic differentiation within and across bioregions along the South African coastline. The most recent review on genetic structuring of marine species (Teske et al., 2011) identified phylogeographic breaks that are broadly concurrent with the boundaries between bioregions, but also noted several instances where the two do not overlap. Although structure between bioregions was recognized, patterns within bioregions were not accounted for. Here, we extend previous analyses by comparing genetic structuring within each bioregion, and found that the CT and SW regions display the highest levels of intraspecific structuring on average (Figure 4), with the WT and ST having lower genetic structure. The size of the bioregion and the range in mean SSTs were found to have no significant effect on Φ_{ST} values, which suggests that other climatic and/or biogeographic features are driving these patterns. As previously mentioned, the SW region has experienced higher sea-level changes since the LGM, and is a location with strong contemporary biogeographic breaks most likely owing to coastal topography, which could explain the high levels of Φ_{ST} in this region. Furthermore, biophysical modelling within the CT region provides evidence of small-scale oceanographic processes contributing to local-scale larval retention and genetic structuring (Mertens et al., 2018). This, in combination with geographic distance and mean SST variation showing no significant effect in the linear models, leads us to conclude that the high levels of genetic structure are driven by local oceanographic and biophysical features interacting with life history traits. The Φ_{ST} analyses suggest that the SW coast is of additional conservation importance, with high levels of diversity and differentiation. Thus, further protection within the SW region could enhance multi-species evolutionary potential and conserve different evolutionarily significant units, hence creating reserves that adequately represent the evolutionary dynamics and patterns of the region (Nielsen et al., 2017, 2020).

4.2 | The effects of environment and geography on multi-species evolutionary patterns

Climatic variability and habitat complexity have long been considered important features shaping species diversity patterns (Gagné et al., 2020), but are not as often considered in understanding the processes driving molecular diversity. Recent multispecies studies have assessed these drivers of genetic diversity on a global scale, suggesting that environmental variables such as temperature (Manel et al., 2020) or position within a species' geographic range (De Kort et al., 2021) are important processes shaping genetic diversity. Here, we considered these processes on a more localized

spatial scale, finding that neither mean temperature nor geographic range position significantly co-varies with intraspecific genetic diversity (Table 2). Instead, the linear mixed models revealed that the range in contemporary SSTs is positively correlated with intraspecific haplotype diversity values (Figure 5). This distinction between drivers of genetic diversity highlights how global-scale analyses may not capture biodiversity trends occurring at more localized spatial scales (Sax & Gaines, 2003). Our results also contrast with previous studies within South Africa, which suggest that mean SST (Phair et al., 2019; Teske et al., 2019) and range position (Nielsen, Beger, et al., 2021) are strong drivers of genetic diversity. However, these South African studies were conducted on single species, and thus cannot account for the large differences between species and the broad evolutionary processes shaping multi-species diversity. In our comparative multi-species analysis, it was not mean temperature, but range in temperature, that was significantly correlated with haplotype diversity. Range in temperature being an important driver of genetic diversity is not surprising, as environmental heterogeneity is regarded as one of the most important factors shaping species richness (Stein et al., 2014). This idea can be expanded to the level of genetic diversity by individuals within populations experiencing a higher range of SSTs requiring a larger range of both phenotypic and genetic variation to persist under this type of balancing selection (Banks et al., 2013). Evidence for this hypothesis has been shown by high climatic variability leading to higher levels of intraspecific diversity in bull trout in the Columbia River Basin (Kovach et al., 2015) and differential phenotypic expression in sticklebacks (Garduño-Paz et al., 2010).

In comparison with haplotype diversity, variability in nucleotide diversity did not correlate with any environmental or biogeographic predictor variables, suggesting that different diversity statistics reflect contrasting evolutionary histories (Epps & Keyghobadi, 2015), and highlighting the importance of comparing different metrics to understand evolutionary processes for conservation. Life-history traits may also render species more sensitive to changes in different molecular metrics, such as long-lived species being more prone to loss of allelic richness, and short-lived species more prone to loss of haplotype diversity (González et al., 2020), although this could not be tested here given the generally poor state of knowledge on the life histories of the marine species investigated here, especially the invertebrates that form the bulk of our study.

Range position was not a significant predictor of either *h* or π. This was unexpected, as distance from the centre of a species' distribution has been shown to be a strong driver of global genetic diversity across taxa (de Kort et al., 2021), as well as being a significant determinant of diversity for single species within South Africa (Nielsen et al., 2020). However, evidence for the core-edge hypothesis remains highly inconsistent (Dallas & Santini, 2020; Lira-Noriega & Manthey, 2014) and is probably largely influenced by life-history traits (Ellegren & Galtier, 2016). For example, many of the species included here have high dispersal capabilities and broad geographic

ranges, making them less likely to display an abundant-centre pattern in genetic diversity (Ntuli et al., 2020).

Habitat (here broadly classified into soft and hard substrates) also had no significant effect on diversity in the mixed linear models, corroborating the results of Dalongeville et al. (2016) in the Mediterranean Sea, who found that habitat types (soft, rocky and seagrass beds) showed no significant correlation with the genetic diversity of 13 fish species. Habitat availability is thought to be a crucial component in genetic differentiation (Binks et al., 2019), but this is probably a less important factor in this system, as hard and soft substrates are evenly distributed throughout the region (Tolley et al., 2019) and habitat types are not always clearly differentiated. For example, approximately 42% of South Africa's coastline comprises 'mixed shore', that is, it has both rocky and sandy components.

The additional predictors 'bioregion size' and 'range in mean SSTs' had no effect on Φ_{ST}, even though the latter was an important predictor for patterns of diversity. It is likely that a combination of life-history traits and near-shore oceanographic currents influences patterns of within-bioregion genetic structuring (Iacchei et al., 2013; Orsini et al., 2013; C. Sjöqvist et al., 2015), but these data are unfortunately largely unavailable for the region and many of the species. While the effects of life history, biogeography, temperature and oceanographic features on genetic diversity of South African marine species have been explored (Nielsen, Henriques, et al., 2021; Phair et al., 2020; Teske et al., 2011), they are rarely combined into multivariate, multispecies analyses. These types of integrative studies are needed to capture the complex spatio-temporal interactions shaping the diversity along this dynamic coastline.

Our study suggests that factors shown to influence global genetic diversity patterns, mainly temperature (Manel et al., 2020) and range position (de Kort et al., 2021), may not be as strong of predictors of multi-species genetic variation on smaller spatial scales. However, our study does have some limitations which may have led to the lack of strong predictors of significant associations between genetic diversity and environmental and biogeographic variation. For instance, we were limited in only using data from mtDNA markers, as other marker types, such as genome-wide SNPs, do not exist for as wide an array of taxa within the region. Furthermore, both *h* or π scale not only by population size, but also by mutation rate, which may be why we did not find simple relationships with genetic diversity and ecological variation. We were constrained by many studies having sampled few individuals at many sites, and after applying a set of filtering criteria in order to account for unbalanced sampling, we were left with smaller sample sizes. Understanding the amount of data sufficient to capture multi-species evolutionary patterns remains difficult, as power analyses used to model species–area relationships are not always suited to determine sufficient sampling genetic diversity assessments (Phillips et al., 2019). Our limitations in available molecular information, species and regions sampled and detailed life-history traits of study species, highlight important knowledge gaps in the region, which should be prioritized to further characterize the phylogeography of this marine biodiversity hotspot.

4.3 | The future of molecular research on southern Africa's marine realm

Ten years ago, Teske et al. (2011) provided the first comprehensive overview of genetic studies conducted on southern African marine organisms, where they recognized the link between species-level biogeographic transition areas and infraspecific phylogeographic breaks. They also noted that the CT and tropical bioregions had been poorly studied at the time. In our analyses, we found that genetic information available for the CT bioregion is now much improved, but that the tropical bioregion remains in need of further phylogeographic study. Indeed, the tropical bioregion was not included in this study due to a lack of suitable data. Additionally, studies with sampling domains spanning both South Africa and the neighbouring countries (Namibia in the west and Mozambique in the east) are limited, but will be vital to identify many of the potential intraspecific lineages that may remain undescribed (Beheregaray, 2008).

Teske et al. (2011) also reported the lack of phylogeographic research conducted on commercially important species, which this study corroborates, with only 37% of the total studies being on exploited species. Yet, there has been notable progress with regard to both the number of species and the number of molecular markers included in recent population genetic studies in South Africa, with 38 studies including multiple markers at the time of the literature search, and many also including multiple species. Arguably, the most significant advancement in molecular research is the advent of genomic analyses; yet, the number of available genome-wide datasets in South Africa is a magnitude lower than genetic datasets, and rarely exists for multiple species (Tolley et al., 2019). Going forward, we expect to see an increase in the use of genomic markers, as these not only have much greater power to detect genetic structure by means of selectively neutral markers but can also be used to identify gene–environment interactions and highlight intraspecific adaptive signals (Helyar et al., 2011). As neutral and adaptive genetic patterns have been shown to differ (Boulanger et al., 2021; Liggins et al., 2020; Milano et al., 2014; Torrado et al., 2020), comparing adaptive signals across multiple taxa would provide an interesting addition to the present study, and could allow identifying environmental and climatic features causing local adaptation of marine species. For example, Nielsen, Henriques, et al. (2021) showed that genomic vulnerability under climatic change differs between sympatric species requiring alternative solutions for protecting intraspecific diversity.

South Africa is one of the leading countries to integrate molecular data into conservation planning frameworks (Nielsen et al., 2017; Rouget et al., 2003; Scoble & Lowe, 2010; von der Heyden, 2009). We believe that the uniquely situated South African coastline will continue to supply novel insights into the genetic and genomic consequences of global climate change in the temperate southern

hemisphere, with data informing conservation policies in this highly biodiverse marine realm.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code are publicly available on the following GitHub repository: https://github.com/AliciaDalongeville/MolecularReview.git

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REFERENCES

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & Clerck, O. D. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27(3), 277–284. https://doi.org/10.1111/geb.12693

Awad, A. A., Griffiths, C. L., & Turpie, J. K. (2002). Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. *Diversity and Distributions*, 8(3), 129–145. https://doi.org/10.1046/j.1472-4642.2002.00132.x

Banks, S. C., Cary, G. J., Smith, A. L., Davies, I. D., Driscoll, D. A., Gill, A. M., Lindenmayer, D. B., & Peakall, R. (2013). How does ecological disturbance influence genetic diversity? *Trends in Ecology & Evolution*, 28(11), 670–679. https://doi.org/10.1016/j.tree.2013.08.005

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48.

Beger, M., Selkoe, K. A., Treml, E., Barber, P. H., von derHeyden, S., Crandall, E. D., Toonen, R. J., & Riginos, C. (2014). Evolving coral reef conservation with genetic information. *Bulletin of Marine Science*, 90(1), 159–185. https://doi.org/10.5343/bms.2012.1106

Beheregaray, L. B. (2008). Twenty years of phylogeography: The state of the field and the challenges for the Southern Hemisphere. *Molecular Ecology*, 17(17), 3754–3774. https://doi.org/10.1111/j.1365-294X.2008.03857.x

Binks, R. M., Byrne, M., McMahon, K., Pitt, G., Murray, K., & Evans, R. D. (2019). Habitat discontinuities form strong barriers to gene flow among mangrove populations, despite the capacity for long-distance dispersal. *Diversity and Distributions*, 25(2), 298–309. https://doi.org/10.1111/ddi.12851

Boulanger, E., Benestan, L., Guerin, P.-E., Dalongeville, A., Mouillot, D., & Manel, S. (2021). Climate differently influences the genomic patterns of two sympatric marine fish species. *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.13623

Bowen, B. W., Shanker, K., Yasuda, N., Celia, M., Malay, M. C., von der-Heyden, S., Paulay, G., Rocha, L. A., Selkoe, K. A., Barber, P. H., Williams, S. T., Lessios, H. A., Crandall, E. D., Bernardi, G., Meyer, C. P., Carpenter, K. E., & Toonen, R. J. (2014). Phylogeography unplugged: Comparative surveys in the genomic era. *Bulletin of Marine Science*, 90(1), 13–46. https://doi.org/10.5343/bms.2013.1007

Branch, G., & Branch, M. (2018). *Living shores* (Revised edition). Penguin Random House South Africa.

Branch, G., Branch, M., Griffiths, C. L., & Beckley, L. E. (2016). *Two oceans: A guide to the marine life of Southern Africa*, 4th ed. Struik Nature.

Carnaval, A. C., Hickerson, M. J., Haddad, C. F., Rodrigues, M. T., & Moritz, C. (2009). Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, 323(5915), 785–789.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114(30), 201704949. https://doi.org/10.1073/pnas.1704949114

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: towards a Predictive Theory. *PLoS Biology*, 8(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Crandall, E. D., Riginos, C., Bird, C. E., Liggins, L., Treml, E., Beger, M., Barber, P. H., Connolly, S. R., Cowman, P. F., DiBattista, J. D., Eble, J. A., Magnuson, S. F., Horne, J. B., Kochzius, M., Lessios, H. A., Liu, S. Y. V., Ludt, W. B., Madduppa, H., Pandolfi, J. M., ... Gaither, M. R. (2019). The molecular biogeography of the Indo-Pacific: Testing hypotheses with multispecies genetic patterns. *Global Ecology and Biogeography*, 28(7), 943–960. https://doi.org/10.1111/geb.12905

Dallas, T. A., & Santini, L. (2020). The influence of stochasticity, landscape structure and species traits on abundant–centre relationships. *Ecography*, 43(9), 1341–1351. https://doi.org/10.1111/ecog.05164

Dalongeville, A., Andrello, M., Mouillot, D., Albouy, C., & Manel, S. (2016). Ecological traits shape genetic diversity patterns across the Mediterranean Sea: A quantitative review on fishes. *Journal of Biogeography*, 43(4), 845–857. https://doi.org/10.1111/jbi.12669

De Kort, H., Prunier, J. G., Ducatez, S., Honnay, O., Baguette, M., Stevens, V. M., & Blanchet, S. (2021). Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. *Nature Communications*, 12(1), 516. https://doi.org/10.1038/s41467-021-20958-2

DeWoody, J. A., Harder, A. M., Mathur, S., & Willoughby, J. R. (2021). The long-standing significance of genetic diversity in conservation. *Molecular Ecology*, 30(17), 4147–4154. https://doi.org/10.1111/mec.16051

Dinno, A. (2017). *Dunn's test of multiple comparisons using rank sums (1.3.5)*. [Computer software].

DuBois, K., Williams, S. L., & Stachowicz, J. J. (2021). Experimental warming enhances effects of eelgrass genetic diversity via temperature-induced niche differentiation. *Estuaries and Coasts*, 44(2), 545–557. https://doi.org/10.1007/s12237-020-00827-9

Dunn, O. J. (1964). Multiple comparisons using rank sums. *Technometrics*, 6(3), 241–252. https://doi.org/10.1080/00401706.1964.10490181

Eckert, C. G., Samis, K. E., & Lougheed, S. C. (2008). Genetic variation across species' geographical ranges: The central–marginal hypothesis and beyond. *Molecular Ecology*, 17(5), 1170–1188. https://doi.org/10.1111/j.1365-294X.2007.03659.x

Ellegren, H., & Galtier, N. (2016). Determinants of genetic diversity. *Nature Reviews Genetics*, 17(7), 422–433. https://doi.org/10.1038/nrg.2016.58

Epps, C. W., & Keyghobadi, N. (2015). Landscape genetics in a changing world: Disentangling historical and contemporary influences and inferring change. *Molecular Ecology*, 24(24), 6021–6040. https://doi.org/10.1111/mec.13454

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under

Linux and Windows. *Molecular Ecology Resources*, *10*(3), 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Excoffier, L., Smouse, P., & Quattro, J. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, *131*, 479–491. https://doi.org/10.1093/genetics/131.2.479

Fai, A.- H.-T., & Cornelius, P. L. (1996). Approximate F-tests of multiple degree of freedom hypotheses in generalized least squares analyses of unbalanced split-plot experiments. *Journal of Statistical Computation and Simulation*, *54*(4), 363–378. https://doi.org/10.1080/00949659608811740

Frankham, R. (1995). Conservation genetics. *Annual Review of Genetics*, *29*, 305–327. https://doi.org/10.1146/annurev.ge.29.120195.001513

Gagné, T. O., Reygondeau, G., Jenkins, C. N., Sexton, J. O., Bograd, S. J., Hazen, E. L., & Houtan, K. S. V. (2020). Towards a global understanding of the drivers of marine and terrestrial biodiversity. *PLoS One*, *15*(2), e0228065. https://doi.org/10.1371/journal.pone.0228065

Garduño-Paz, M. V., Couderc, S., & Adams, C. E. (2010). Habitat complexity modulates phenotype expression through developmental plasticity in the threespine stickleback. *Biological Journal of the Linnean Society*, *100*(2), 407–413. https://doi.org/10.1111/j.1095-8312.2010.01423.x

González, A. V., Gómez-Silva, V., Ramírez, M. J., & Fontúrbel, F. E. (2020). Meta-analysis of the differential effects of habitat fragmentation and degradation on plant genetic diversity. *Conservation Biology*, *34*(3), 711–720. https://doi.org/10.1111/cobi.13422

Goodall-Copestake, W. P., Tarling, G. A., & Murphy, E. J. (2012). On the comparison of population-level estimates of haplotype and nucleotide diversity: A case study using the gene cox1 in animals. *Heredity*, *109*(1), 50–56. https://doi.org/10.1038/hdy.2012.12

Gratton, P., Marta, S., Bocksberger, G., Winter, M., Keil, P., Trucchi, E., & Kühl, H. (2017). Which latitudinal gradients for genetic diversity? *Trends in Ecology & Evolution*, *32*(10), 724–726. https://doi.org/10.1016/j.tree.2017.07.007

Griffiths, C. L., Robinson, T. B., Lange, L., & Mead, A. (2010). Marine biodiversity in South Africa: An evaluation of current states of knowledge. *PLoS One*, *5*(8), e12008. https://doi.org/10.1371/journal.pone.0012008

Hale, M. L., Burg, T. M., & Steeves, T. E. (2012). Sampling for microsatellite-based population genetic studies: 25 to 30 individuals per population is enough to accurately estimate Allele frequencies. *PLoS One*, *7*(9), e45170. https://doi.org/10.1371/journal.pone.0045170

Hanson, B., & Seeger, C. (2017). QGIS: Road Graph Plugin - Finding Shortest Path. GIS and Mapping Task Sheets. Available from https://lib.dr.iastate.edu/gis_tasksheets/6

Helyar, S. J., Hemmer-Hansen, J., Bekkevold, D., Taylor, M. I., Ogden, R., Limborg, M. T., Cariani, A., Maes, G. E., Diopere, E., Carvalho, G. R., & Nielsen, E. E. (2011). Application of SNPs for population genetics of nonmodel organisms: New opportunities and challenges. *Molecular Ecology Resources*, *11*(Suppl 1), 123–136. https://doi.org/10.1111/j.1755-0998.2010.02943.x

Henriques, R., Mann, B., Nielsen, E., Hui, C., & von derHeyden, S. (2020). Extending biodiversity conservation with functional and evolutionary diversity: A case study of South African sparid fishes. *African Journal of Marine Science*, *42*(3), 315–321. https://doi.org/10.2989/1814232X.2020.1798282

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, *405*(6789), 907–913. https://doi.org/10.1038/35016000

Hillebrand, H., Jacob, U., & Leslie, H. M. (2020). Integrative research perspectives on marine conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1814), 20190444. https://doi.org/10.1098/rstb.2019.0444

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, *11*(6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

Iacchei, M., Ben-Horin, T., Selkoe, K. A., Bird, C. E., García-Rodríguez, F. J., & Toonen, R. J. (2013). Combined analyses of kinship and FST suggest potential drivers of chaotic genetic patchiness in high gene-flow populations. *Molecular Ecology*, *22*(13), 3476–3494. https://doi.org/10.1111/mec.12341

Kimura, M. (1985). *The Neutral Theory of Molecular Evolution*. Cambridge University Press.

Kovach, R. P., Muhlfeld, C. C., Wade, A. A., Hand, B. K., Whited, D. C., DeHaan, P. W., Al-Chokhachy, R., & Luikart, G. (2015). Genetic diversity is related to climatic variation and vulnerability in threatened bull trout. *Global Change Biology*, *21*(7), 2510–2524. https://doi.org/10.1111/gcb.12850

Kruskal, W. H., & Wallis, W. A. (1952). Use of ranks in one-vriterion variance analysis. *Journal of the American Statistical Association*, *47*(260), 583–621. https://doi.org/10.2307/2280779

Kuo, C.-H., & Avise, J. C. (2005). Phylogeographic breaks in low-dispersal species: the emergence of concordance across gene trees. *Genetica*, *124*(2), 179–186. https://doi.org/10.1007/s10709-005-2095-y

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26.

Liggins, L., Treml, E. A., & Riginos, C. (2020). Seascape Genomics: contextualizing adaptive and neutral genomic variation in the ocean environment. In M. F.Oleksiak, & O. P.Rajora (Eds.), *Population genomics: Marine organisms* (pp. 171–218). Springer International Publishing. https://doi.org/10.1007/13836_2019_68

Lira-Noriega, A., & Manthey, J. D. (2014). Relationship of genetic diversity and niche centrality: A Survey and Analysis. *Evolution*, *68*(4), 1082–1093. https://doi.org/10.1111/evo.12343

Ludt, W. B., & Rocha, L. A. (2015). Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. *Journal of Biogeography*, *42*(1), 25–38. https://doi.org/10.1111/jbi.12416

Maggs, C. A., Castilho, R., Foltz, D., Henzler, C., Jolly, M. T., Kelly, J., Olsen, J., Perez, K. E., Stam, W., Väinölä, R., Viard, F., & Wares, J. (2008). Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology*, *89*(sp11), S108–S122. https://doi.org/10.1890/08-0257.1

Manel, S., Guerin, P.-E., Mouillot, D., Blanchet, S., Velez, L., Albouy, C., & Pellissier, L. (2020). Global determinants of freshwater and marine fish genetic diversity. *Nature Communications*, *11*(1), 692. https://doi.org/10.1038/s41467-020-14409-7

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405*(6783), 243–253. https://doi.org/10.1038/35012251

Mertens, L. E. A., Treml, E. A., & von derHeyden, S. (2018). Genetic and biophysical models help define marine conservation focus areas. *Frontiers in Marine Science*, *5*, https://doi.org/10.3389/fmars.2018.00268

Milano, I., Babbucci, M., Cariani, A., Atanassova, M., Bekkevold, D., Carvalho, G. R., Espiñeira, M., Fiorentino, F., Garofalo, G., Geffen, A. J., & Hansen, J. H., Helyar, S. J., Nielsen, E. E., Ogden, R., Patarnello, T., Stagioni, M., FishPopTrace Consortium, Tinti, F., & Bargelloni, L. (2014). Outlier SNP markers reveal fine-scale genetic structuring across European hake populations (*Merluccius merluccius*). *Molecular Ecology*, *23*(1), 118–135. https://doi.org/10.1111/mec.12568

Miraldo, A., Li, S., Borregaard, M. K., Flórez-Rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., Wang, Z., Rahbek, C., Marske, K. A., & Nogués-Bravo, D. (2016). An Anthropocene map of genetic diversity. *Science*, *353*(6307), 1532–1535. https://doi.org/10.1126/science.aaf4381

Moilanen, A., Wilson, K. A., & Possingham, H. P. (2009). *Spatial Conservation Prioritization*. Oxford University Press. https://global.oup.com/academic/product/spatial-conservation-prioritization-9780199547777

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M.,

Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M., & Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature*, *502*(7470), 183–187. https://doi.org/10.1038/nature12540

Nei, M. (1987). *Molecular evolutionary genetics*. Columbia University Press.

Nielsen, E. S., Beger, M., Henriques, R., Selkoe, K. A., & von derHeyden, S. (2017). Multispecies genetic objectives in spatial conservation planning. *Conservation Biology*, *31*(4), 872–882. https://doi.org/10.1111/cobi.12875

Nielsen, E. S., Beger, M., Henriques, R., & von derHeyden, S. (2020). A comparison of genetic and genomic approaches to represent evolutionary potential in conservation planning. *Biological Conservation*, *251*, 108770. https://doi.org/10.1016/j.biocon.2020.108770

Nielsen, E. S., Beger, M., Henriques, R., & von derHeyden, S. (2021). Neither historical climate nor contemporary range fully explain the extant patterns of molecular diversity in marine species. *Journal of Biogeography*, *48*(10), 2629–2644. https://doi.org/10.1111/jbi.14229

Nielsen, E. S., Henriques, R., Beger, M., & von derHeyden, S. (2021). Distinct interspecific and intraspecific vulnerability of coastal species to global change. *Global Change Biology*, *27*(15), 3415–3431. https://doi.org/10.1111/gcb.15651

Ntuli, N. N., Nicastro, K. R., Zardi, G. I., Assis, J., McQuaid, C. D., & Teske, P. R. (2020). Rejection of the genetic implications of the "Abundant Centre Hypothesis" in marine mussels. *Scientific Reports*, *10*(1), 604. https://doi.org/10.1038/s41598-020-57474-0

Nunney, L. (1993). The influence of mating system and overlapping generations on effective population size. *Evolution*, *47*(5), 1329–1341. https://doi.org/10.2307/2410151

Orsini, L., Vanoverbeke, J., Swillen, I., Mergeay, J., & De Meester, L. (2013). Drivers of population genetic differentiation in the wild: Isolation by dispersal limitation, isolation by adaptation and isolation by colonization. *Molecular Ecology*, *22*(24), 5983–5999. https://doi.org/10.1111/mec.12561

Page, T. J., & Hughes, J. M. (2014). Contrasting insights provided by single and multispecies data in a regional comparative phyogeographic study. *Biological Journal of the Linnean Society*, *111*(3), 554–569. https://doi.org/10.1111/bij.12231

Panetta, A. M., Stanton, M. L., & Harte, J. (2018). Climate warming drives local extinction: Evidence from observation and experimentation. *Science Advances*, *4*(2), eaaq1819. https://doi.org/10.1126/sciadv.aaq1819

Pascual, M., Rives, B., Schunter, C., & Macpherson, E. (2017). Impact of life history traits on gene flow: A multispecies systematic review across oceanographic barriers in the Mediterranean Sea. *PLoS One*, *12*(5), e0176419. https://doi.org/10.1371/journal.pone.0176419

Phair, N. L., Nielsen, E. S., & von derHeyden, S. (2021). Applying genomic data to seagrass conservation. *Biodiversity and Conservation*, *30*(7), 2079–2096. https://doi.org/10.1007/s10531-021-02184-w

Phair, N. L., Toonen, R. J., Knapp, I., & von derHeyden, S. (2019). Shared genomic outliers across two divergent population clusters of a highly threatened seagrass. *PeerJ*, *7*, e6806. https://doi.org/10.7717/peerj.6806

Phair, N. L., Toonen, R. J., Knapp, I. S. S., & von derHeyden, S. (2020). Anthropogenic pressures negatively impact genomic diversity of the vulnerable seagrass Zostera capensis. *Journal of Environmental Management*, *255*, 109831. https://doi.org/10.1016/j.jenvman.2019.109831

Phillips, J. D., Gillis, D. J., & Hanner, R. H. (2019). Incomplete estimates of genetic diversity within species: Implications for DNA barcoding. *Ecology and Evolution*, *9*(5), 2996–3010. https://doi.org/10.1002/ece3.4757

Pianka, E. R. (1996). *Long-term changes in lizard assemblages in the Great Victoria Desert. Long-term studies of vertebrate communities (ML Cody and JA Smallwood, eds.)* (pp. 191–215). Academic Press.

Provan, J., & Bennett, K. D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution*, *23*(10), 564–571. https://doi.org/10.1016/j.tree.2008.06.010

Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: A meta-analysis. *Biological Reviews*, *94*(2), 648–661. https://doi.org/10.1111/brv.12472

Ramsay, P. J., & Cooper, J. A. G. (2002). Late Quaternary sea-level change in South Africa. *Quaternary Research*, *57*(1), 82–90. https://doi.org/10.1006/qres.2001.2290

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: How spatial analyses can augment population genomic studies. *Current Zoology*, *62*(6), 581–601. https://doi.org/10.1093/cz/zow067

Rouget, M., Richardson, D. M., Cowling, R. M., Lloyd, J. W., & Lombard, A. T. (2003). Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation*, *112*(1), 63–85. https://doi.org/10.1016/S0006-3207(02)00395-6

Ryman, N., Allendorf, F. W., Jorde, P. E., Laikre, L., & Hössjer, O. (2014). Samples from subdivided populations yield biased estimates of effective size that overestimate the rate of loss of genetic variation. *Molecular Ecology Resources*, *14*(1), 87–99. https://doi.org/10.1111/1755-0998.12154

Salo, T., & Gustafsson, C. (2016). The Effect of Genetic Diversity on Ecosystem Functioning in Vegetated Coastal Ecosystems. *Ecosystems*, *19*(8), 1429–1444. https://doi.org/10.1007/s10021-016-0014-y

Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution*, *18*(11), 561–566. https://doi.org/10.1016/S0169-5347(03)00224-6

Sbrocco, E. J. (2014). Paleo-MARSPEC: Gridded ocean climate layers for the mid-Holocene and Last Glacial Maximum. *Ecology*, *95*(6), 1710. https://doi.org/10.1890/14-0443.1

Schiebelhut, L. M., & Dawson, M. N. (2018). Correlates of population genetic differentiation in marine and terrestrial environments. *Journal of Biogeography*, *45*(11), 2427–2441. https://doi.org/10.1111/jbi.13437

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257–263. https://doi.org/10.1890/140275

Schunter, C., Carreras-Carbonell, J., Macpherson, E., Tintoré, J., Vidal-Vijande, E., Pascual, A., Guidetti, P., & Pascual, M. (2011). Matching genetics with oceanography: Directional gene flow in a Mediterranean fish species. *Molecular Ecology*, *20*(24), 5167–5181. https://doi.org/10.1111/j.1365-294X.2011.05355.x

Scoble, J., & Lowe, A. J. (2010). A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning: Incorporating molecular marker information into species modelling. *Diversity and Distributions*, *16*(3), 343–353. https://doi.org/10.1111/j.1472-4642.2010.00658.x

Selkoe, K., D'Aloia, C., Crandall, E., Iacchei, M., Liggins, L., Puritz, J., von derHeyden, S., & Toonen, R. (2016). A decade of seascape genetics: Contributions to basic and applied marine connectivity. *Marine Ecology Progress Series*, *554*, 1–19. https://doi.org/10.3354/meps11792

Selkoe, K. A., Gaggiotti, O. E., Bowen, B. W., & Toonen, R. J. (2014). Emergent patterns of population genetic structure for a coral reef community. *Molecular Ecology*, *23*(12), 3064–3079. https://doi.org/10.1111/mec.12804

Sjöqvist, C., Godhe, A., Jonsson, P. R., Sundqvist, L., & Kremp, A. (2015). Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea-Baltic Sea salinity gradient. *Molecular Ecology*, *24*(11), 2871–2885. https://doi.org/10.1111/mec.13208

Sjöqvist, C. O., & Kremp, A. (2016). Genetic diversity affects ecological performance and stress response of marine diatom populations. *The ISME Journal*, *10*(11), 2755–2766. https://doi.org/10.1038/ismej.2016.44

Stange, M., Barrett, R. D. H., & Hendry, A. P. (2021). The importance of genomic variation for biodiversity, ecosystems and people. *Nature Reviews Genetics*, *22*(2), 89–105. https://doi.org/10.1038/s41576-020-00288-7

Stanley, R. R. E., DiBacco, C., Lowen, B., Beiko, R. G., Jeffery, N. W., Van Wyngaarden, M., Bentzen, P., Brickman, D., Benestan, L., Bernatchez, L., Johnson, C., Snelgrove, P. V. R., Wang, Z., Wringe, B. F., & Bradbury, I. R. (2018). A climate-associated multispecies cryptic cline in the northwest Atlantic. *Science Advances*, *4*(3), eaaq0929. https://doi.org/10.1126/sciadv.aaq0929

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866–880. https://doi.org/10.1111/ele.12277

Tamura, K., & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, *10*(3), 512–526. https://doi.org/10.1093/oxfordjournals.molbev.a040023

Teixeira, J. C., & Huber, C. D. (2021). The inflated significance of neutral genetic diversity in conservation genetics. *Proceedings of the National Academy of Sciences*, *118*(10), https://doi.org/10.1073/pnas.2015096118

Teske, P. R., Emami-Khoyi, A., Golla, T. R., Sandoval-Castillo, J., Lamont, T., Chiazzari, B., McQuaid, C. D., Beheregaray, L. B., & van der Lingen, C. D. (2021). The sardine run in southeastern Africa is a mass migration into an ecological trap. *Science Advances*, *7*(38), eabf4514. https://doi.org/10.1126/sciadv.abf4514

Teske, P. R., Sandoval-Castillo, J., Golla, T. R., Emami-Khoyi, A., Tine, M., von derHeyden, S., & Beheregaray, L. B. (2019). Thermal selection as a driver of marine ecological speciation. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1896), 20182023. https://doi.org/10.1098/rspb.2018.2023

Teske, P. R., von derHeyden, S., McQuaid, C. D., & Barker, N. P. (2011). A review of marine phylogeography in southern Africa. *South African Journal of Science*, *107*(5/6), 1–11. https://doi.org/10.4102/sajs.v107i5/6.514

Thomson, A. I., Archer, F. I., Coleman, M. A., Gajardo, G., Goodall-Copestake, W. P., Hoban, S., Laikre, L., Miller, A. D., O'Brien, D., Pérez-Espona, S., Segelbacher, G., Serrão, E. A., Sjøtun, K., & Stanley, M. S. (2021). Charting a course for genetic diversity in the UN decade of ocean science. *Evolutionary Applications*, *14*(6), 1497–1518. https://doi.org/10.1111/eva.13224

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*(7310), 1098–1101.

Tolley, K., Da Silva, J., & Jansen van Vuuren, B. (2019). *South African National Biodiversity Assessment 2018 Technical Report Volume 7: Genetic Diversity*. Available from http://opus.sanbi.org:80/jspui/handle/20.500.12143/6376

Toms, J. A., Compton, J. S., Smale, M., & von derHeyden, S. (2014). Variation in palaeo-shorelines explains contemporary population genetic patterns of rocky shore species. *Biology Letters*, *10*(6), 20140330. https://doi.org/10.1098/rsbl.2014.0330

Torrado, H., Carreras, C., Raventos, N., Macpherson, E., & Pascual, M. (2020). Individual-based population genomics reveal different drivers of adaptation in sympatric fish. *Scientific Reports*, *10*(1), 12683. https://doi.org/10.1038/s41598-020-69160-2

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & Clerck, O. D. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

von derHeyden, S. (2009). Why do we need to integrate population genetics into South African marine protected area planning? *African Journal of Marine Science*, *31*(2), 263–269. https://doi.org/10.2989/AJMS.2009.31.2.14.886

von derHeyden, S. (2017). Making evolutionary history count: Biodiversity planning for coral reef fishes and the conservation of evolutionary processes. *Coral Reefs*, *36*(1), 183–194. https://doi.org/10.1007/s00338-016-1512-2

von derHeyden, S., Prochazka, K., & Bowie, R. C. K. (2008). Significant population structure and asymmetric gene flow patterns amidst expanding populations of *Clinus cottoides* (Perciformes, Clinidae): Application of molecular data to marine conservation planning in South Africa. *Molecular Ecology*, *17*(22), 4812–4826. https://doi.org/10.1111/j.1365-294X.2008.03959.x

Wagner, H. H., & Fortin, M.-J. (2013). A conceptual framework for the spatial analysis of landscape genetic data. *Conservation Genetics*, *14*(2), 253–261. https://doi.org/10.1007/s10592-012-0391-5

Wares, J. P. (2002). Community genetics in the Northwestern Atlantic intertidal. *Molecular Ecology*, *11*(7), 1131–1144. https://doi.org/10.1046/j.1365-294X.2002.01510.x

Webster, M. S., Colton, M. A., Darling, E. S., Armstrong, J., Pinsky, M. L., Knowlton, N., & Schindler, D. E. (2017). Who should pick the winners of climate change? *Trends in Ecology & Evolution*, *32*(3), 167–173. https://doi.org/10.1016/j.tree.2016.12.007

Wright, D., Bishop, J. M., Matthee, C. A., & von derHeyden, S. (2015). Genetic isolation by distance reveals restricted dispersal across a range of life histories: Implications for biodiversity conservation planning across highly variable marine environments. *Diversity and Distributions*, *21*(6), 698–710. https://doi.org/10.1111/ddi.12302

Wyborn, C., & Evans, M. C. (2021). Conservation needs to break free from global priority mapping. *Nature Ecology & Evolution*, *5*(10), 1322–1324. https://doi.org/10.1038/s41559-021-01540.-x

BIOSKETCH

AD uses molecular tools to understand how fish communities respond to environmental and human disturbances. ESN is interested in understanding how marine species are responding to global change, and how to best conserve species under rapid climatic change. PRT and SvdH utilize molecular tools to understand the evolutionary dynamics and conservation of southern African marine species.

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