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Nielsen, ES, Henriques, R, Beger, M orcid.org/0000-0003-1363-3571 et al. (1 more author) (2021) Distinct interspecific and intraspecific vulnerability of coastal species to global change. Global Change Biology. ISSN 1354-1013

https://doi.org/10.1111/gcb.15651

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Distinct inter- and intra-specific vulnerability of coastal species to global change

Running head: Species and population level vulnerability

Authors: Erica S. Nielsen[1], Romina Henriques[1,2], Maria Beger[3], Sophie von der Heyden[1]

Affiliations:
[1]Evolutionary Genomics Group, Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa
[2]Technical University of Denmark, National Institute of Aquatic Resources, Section for Marine Living Resources, Velsøvej 39, Silkeborg, 8600, Denmark
[3]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK

Corresponding author: Erica S. Nielsen
Phone: +27 (0)21 808 3229
Email: esnielsen@sun.ac.za

Keywords: seascape genomics, ecological modelling, species distribution models, gradient forest, adaptive potential, marine invertebrates, climate change, genomic offset

Primary Research Article

Acknowledgements
This project was funded by NRF grants 92788 and 105842. RH was funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Individual Fellowship (837990-DiMaS-H2020-MSCA-IF-2018). We also thank N. Phair for her assistance with the species distribution models, and M. Miller for sharing code for the convex hulls.

Abstract

Characterising and predicting species responses to anthropogenic global change is one of the key challenges in contemporary ecology and conservation. The sensitivity of marine species to climate change is increasingly being described with forecasted species distributions, yet these rarely account for population level processes such as genomic variation and local adaptation. This study compares inter- and intra-specific patterns of biological composition to determine how vulnerability to climate change, and its environmental drivers, vary across species and populations. We compare species trajectories for three ecologically important southern African marine invertebrates at two time points in the future, both at the species level, with correlative species distribution models, and at the population level, with gradient forest models. Reported range shifts are species-specific and include both predicted range gains and losses. Forecasted species responses to climate change are strongly influenced by changes in a suite of environmental variables, from sea surface salinity and sea surface temperature, to minimum air temperature. Our results further suggest a mismatch between future habitat suitability (where species can remain in their ecological niche) and genomic vulnerability (where populations retain their genomic composition), highlighting the inter- and intraspecific variability in species' sensitivity to global change. Overall, this study demonstrates the importance of considering species and population level climatic vulnerability when proactively managing coastal marine ecosystems in the Anthropocene.

Introduction

Anthropogenic climate change is causing worldwide species redistributions and local extinctions, altering community compositions and ecosystem functioning (Babcock et al., 2019; Román-Palacios & Wiens, 2020). As global environmental change forces species to adapt or shift their distributional ranges, conservation actions need to anticipate individual species' responses, and how these will in turn affect ecosystem functioning and human wellbeing (Bonebrake et al., 2018; Pecl et al., 2017; Tittensor et al., 2019). Thus, one of the emerging objectives within conservation science is to protect areas of heightened evolutionary potential (i.e. increased genomic diversity and/or pre-adapted individuals; Funk et al., 2019; Razgour et al., 2019), which requires vulnerability assessments from methods such as physiological experiments, land- or seascape genomics, or forecasting species distribution models (Grummer et al., 2019; Wilson et al., 2020).

A taxon's vulnerability to climate change is often assessed with species distribution models (SDMs; Guisan & Thuiller, 2005) that predict the probability of occurrence from correlations between known occurrences and environmental variables (Elith & Leathwick, 2009). However, most assessments of species range shifts from SDMs disregard the occurrence of intraspecific climatic tolerances, local adaptation, and gene flow (Rilov et al., 2019). This is problematic, as genetic variation is a crucial component of a species' resilience, with areas of high neutral diversity inferring more raw material for adaptation to occur, and high adaptive diversity inferring pre-adapted populations (Bitter et al., 2019; Nielsen et al., 2020a). There have been efforts to assess lineage (D'Amen et al., 2013; Espíndola et al., 2012) and population (Banta et al., 2012; Jay et al., 2012) level responses to climate change with 'genetic SDMs', often showing a disproportionate loss of genetic variation over the species' range. However, to date, most studies including genetic variation in SDMs applied neutral loci to delineate population level variation, which may not capture differentially adapted populations (Mittell et al., 2015). Studies including candidate or 'outlier' loci, i.e. presumed to be under selection, are thus necessary to identify differentially adapted populations (Xuereb et al., 2020). Yet, comparisons of neutral and outlier loci to assess intraspecific vulnerability to global change remains limited, especially in the marine environment. In a recent terrestrial study, Razgour et al. (2019) used outlier loci to identify differentially adapted populations in two bat species, finding that projected distributions into the future differed between populations.

Developing separate SDMs on differentially adapted populations is an important step in understanding the intraspecific responses to future environmental change. However, this methodology does not account for nonlinear gene-environment relationships (Fitzpatrick & Keller, 2015) that are better captured with Gradient Forest (GF) models. Originally used as a community-level approach to predict species assemblages and species turnover (Ellis et al., 2012; Pitcher et al., 2012), GF models can also serve to predict within-species communities, and map areas of 'genomic-turnover' (Fitzpatrick & Keller, 2015). Gradient Forest models can also be used to determine intraspecific 'genomic vulnerability', which is derived from the mismatch between current and future spatial genomic composition (Bay et al., 2018; Morgan et al., 2020). Such approaches to predict intraspecific vulnerability present a hitherto unexplored opportunity to quantify climate change responses in marine species, which are generally more sensitive to warming than terrestrial organisms (Pinsky et al., 2019). Further, comparing the predicted responses to global change across levels of taxonomic organisation with SDMs and GF models has yet to be conducted. Characterising spatio-temporal vulnerability from models accounting for different biological levels is essential to support the identification of climatic refuges for future conservation efforts (Carroll et al., 2017; Morelli et al., 2016).

Here we apply an innovative comparative approach to characterise both intra- and interspecific vulnerability based on species- and gene-environment interactions in the marine environment. This was performed within South Africa, one of the world's most biodiverse marine regions (Griffiths et al., 2010), an ocean warming hotspot (Hobday & Pecl, 2014), and currently underrepresented in marine range shift studies (Sorte et al., 2010). Coastal South Africa is unique, as it is bordered by two contrasting boundary currents, with striking transitions in habitat conditions taking place over relatively short distances (Fig. 1; van der Bank et al., 2019). The coast is composed of five biogeographic regions (Fig. 2), defined by changes in environment (i.e. temperature, salinity, precipitation), habitat type, and species composition (van der Bank et al., 2019). Intraspecific phylogeographic breaks of South African marine species often correlate with these biogeographic breaks, possibly owing to similar environmental features shaping species and genetic level biodiversity patterns (Teske et al., 2011). The region is currently experiencing strong environmental changes, such as an increase in mean annual air temperature (Kruger & Shongwe, 2004), and sea surface temperatures (Rouault et al., 2010). The combination of unique oceanographic features and the marked environmental gradients in this region could easily drive species into vastly different physical conditions and substantially alter community compositions. There are however, few predictions of future species range shifts within this highly unique and threatened marine region (but see Bolton et al., 2012 for an empirical range shift example). Moreover, in other regions of the world, studies suggest species-specific responses to future change (Bates et al., 2014; Sunday et al., 2015), highlighting the need to identify future climatic refuges across multiple species and regions. Thus, this study compares vulnerability patterns across three ecologically important southern African marine invertebrates to identify areas of multispecies evolutionary potential in a known marine biodiversity hotspot. Specifically, this study aims to: 1) characterise spatial genomic composition and predict genomic vulnerability based on neutral and outlier loci per species; 2) predict species distributional shifts into the future, and the environmental drivers of these range shifts, and 3) compare species- and gene-environment relationships and vulnerability footprints between species and populations. We anticipate a mismatch between species and genomic vulnerability, as this has been previously shown within SDMs run at both the species and population level (Jay et al., 2012; Razgour et al., 2019). However, our novel approach directly compares species forecasts from SDMs with genomic forecasts from GF models, the latter of which are capable of capturing complex gene-environment relationships. Here, we expect that areas in which SDMs predict range losses (i.e. high vulnerability) might correlate with areas of low genomic vulnerability, as these populations may be pre-adapted to climatic changes such as warming. Verifying this hypothesis will increase our understanding of how climatic resilience differs between species and populations of co-distributed taxa occurring in a climate change hotspot. More broadly, this work is an essential step in predicting the trajectories of coastal ecosystems under global change.

Materials and Methods

Gradient Forest modelling to infer genomic variation-environment relationships

To infer how climatic variables shape, and will continue to shape, the genomic variation of southern African rocky shore species, allele frequency data from genome-wide single nucleotide polymorphisms (SNPs) was input into Gradient Forest (GF) models. These models assess the relationships between environmental variables and biological abundances by creating an ensemble of individual decision trees (Ellis et al., 2012). More specifically, a machine-learning algorithm is used to partition splits between values of each environmental variable, then calculate the change in allele frequency at each environmental split value, for each allele (Ellis et al., 2012). The amount of variation explained at each split value, termed the ‘split importance’, is summed along the environmental gradient for each allele and aggregated across alleles to create a genome-wide turnover function, per environmental variable.

Gradient Forest models were fitted to the allele frequencies of putatively neutral and outlier SNP datasets for three rocky shore species, the Cape urchin (*Parechinus angulosus*), Common shore crab (*Cyclograpsus punctatus*), and Granular limpet (*Scutellastra granularis*). These species are ecologically important and broadly distributed along the environmental gradients of the southern African coastline, but exhibit different ecological niches and life histories (Branch, 2016; Branch & Branch, 2018). They also have the largest molecular datasets of southern African marine species, spanning four of the five recognised bioregions (Fig. 2). The genomic datasets were previously obtained by Nielsen et al. (2020b) and included ~40 individuals each from 13 to 14 sites for *C. punctatus*, *P. angulosus* and *S. granularis* (Fig. 2). Allele frequency datasets were generated using a pooled restriction siteassociated sequencing (RAD-seq) approach, specifically using ezRAD; ezRAD uniquely allows for a combination of high coverage at specific loci and low coverage across the entire genome (Toonen et al., 2013). To ensure accurate inferences, we included a large number of individuals per pool, and imposed stringent coverage and quality filtering criteria, as well as custom scripts to account for linkage disequilibrium (see Nielsen et al., 2020b for details). Inferences of population differentiation were shown to be robust to changes in bioinformatic filtering parameters such as minimum coverage and read count (Nielsen et al., 2020b). Following the approach of Dalongeville et al., (2018), who used multiple outlier detection models to account for inconsistencies in model assumptions and algorithms, a comprehensive suite of outlier detection methods were used to identify the set of candidate outlier SNPs used here (see Nielsen et al., 2020b for details) to account for and minimize high false discovery rates. Briefly, this involved the use of seven models, consisting of four overarching model types: the auxiliary and core Bayesian hierarchical models of BayPass v.2.1 (Gautier, 2015), Latent Factor Mixed Models (LFMM) of the R package *LEA* (Frichot & François, 2015), Moran Spectral Outlier Detection (MSOD) and Moran Spectral Randomization (MSR) models from the R packages *spdep* and *adespatial* (Bivand et al., 2011; Dray et al., 2017; Wagner et al., 2017), as well as Redundancy Analyses (RDA) and distance-based Redundancy Analyses (dbRDAs) using *vegan* (Oksanen et al., 2013) and *adespatial* R packages (see Nielsen et al., 2020b for further details on each model type and parameters used). The BayPass core model is a genetic differentiation outlier test, while the remaining models are based on genetic-environment association tests (GEAs). Additionally, LFMM is a univariate model, with all other models being multivariate. All model types were chosen as they either use relatedness to account for neutral population structure, or are based on null models of inferred demographic histories, both of which have been shown to lead to more robust outlier identification (Hoban et al., 2016). Moreover, our study system and species are well suited to avoid high false discovery rates in outlier dectection analyses, as there is evidence of high gene flow and demographic homogeneity (Nielsen et al., 2020b), as well as the axes of historical expansion and contemporary environmental variation being aligned in space (Frichot et al., 2015; Muller et al. 2012; Mmonwa et al. 2015).

As there was very little ovelap in outlier loci selected between models (Nielsen et al., 2020b), candidate loci selected by at least two outlier-detection methods were used to create a putative 'outlier dataset' per species, and were removed from the full SNP list to create a putative 'neutral dataset'. It should be noted that even with the thorough approach used here, applying RAD-seq and relatively small SNP datasets to detect candidate loci requires some trade-offs. For example, stringent outlier detection methods may lead to missing true adaptive alleles in the genome, but at the same time their use increases confidence that the identified outlier SNPs represent those at which selection is acting. We tried to navigate this balance by identifying outliers selected by two or more models (to account for false positives), but at the same time using a variety of models (to account for false negatives; Dalongeville et al., 2018; Forester et al., 2018). The neutral datasets consist of 1 177, 810, and 1 632 SNPs, and the outlier datasets consist of 13, 12, and 26 SNPs, for *C. punctatus*, *P. angulosus*, and *S. granularis*, respectively. These allele frequencies served as the response variables in the GF models. The GF models also conduct a form of GEA analysis (i.e. the type of test predominantly used to identify the outlier SNPs stated above), and thus further filtering of the SNPs was performed at that stage, with all those having a goodness-of-fit value $R^2 < 0$ being excluded (see GF methods below for more details).

Eight environmental variables were selected for the GF models based on their importance for rocky shore ecology (Branch & Branch, 2018), marine species distributions (Bosch et al., 2018), and significance in shaping genomic variation within the study species (Nielsen et al., 2020b). These variables were the means and ranges of sea surface temperature (SST), sea surface salinity (SSS), air temperature (T) and precipitation (P). Atmospheric variables were obtained from WorldClim (Fick & Hijmans, 2017) at a ~1km resolution, for three time periods: present day (averaged over 1950-2000), 2050 (averaged over 2041-2060), and 2070 (averaged over 2061-2080). The Community Climate System Model (CCSM4), Hadley Centre Global Environmental Model 2 (HadGEM2-ES) and Model for Interdisciplinary Research on Climate Earth System Model (MIROC-ESM) General Circulation Models (GCMs) were downloaded for atmospheric variables, and cell values were averaged over the GCMs using the 'overlay' function of the *raster* R package (Hijmans et al., 2015). Oceanic variables were obtained from Bio-Oracle2.0 (Assis et al., 2018), at a resolution of ~9km, for present day (averaged over 2000–2014), 2050 (averaged over 2040-2050), and 2100 (averaged over 2090-2100). Within the Bio-Oracle2.0 dataset, oceanic variables were already provided as an ensemble of different GCMs (i.e. averages from CCSM4, HadGEM2-ES and MIROC5 GCMs; see Assis et al., 2018 for details). For all climate model ensemble data, two separate Representative Concentration Pathways (RCPs) were considered for the future variables, namely the intermediate emissions scenario RCP 4.5 and 'worst case' scenario RCP 8.5. For the GF models, the layers pertained to their original resolutions, but for the SDMs (outlined in further detail below), the atmospheric raster layers were resampled to the same cell size of the oceanic variables, using the 'resample' function with the 'nbg' method within the *raster* R package, so that these could be stacked into a single layer.

Since GF models cannot directly accommodate spatial variables, principal coordinates of neighbour matrices (PCNMs) were also included as predictors to account for spatial autocorrelation and unmeasured environmental variation. PCNMs were calculated with the *vegan* R package, and the first half of the positive PCNMs were retained as inputs into the GF models (Manel et al., 2010; Sork et al., 2013). To account for collinearity between environmental predictor variables, we implemented conditional permutations within the GF models, following the protocol outlined by Strobl et al. (2008), using a correlation threshold (r) of 0.5. Default values were used for the number of predictor variables randomly sampled as candidates at each split, number of regression trees fit per allele, and the proportion training and testing samples per tree. Five hundred trees were run per dataset. Gradient Forest models were assessed by the overall goodness-of-fit (R^2) per allele, and the significance of each environmental variable was assessed by the relative importance weighted by R^2 (Martins et al., 2018; Morgan et al., 2020). Only alleles with $R^2>0$ are included in the aggregate turnover function per environmental variable.

Turnover functions from the GF models were used to transform the environmental variables into a common biological importance scale, termed here as 'genomic importance values' (*sensu* Fitzpatrick & Keller 2015). The genomic importance values were mapped in biological and geographic space in a manner similar to ordination, but accounting for non-linear and/or threshold changes that occur within the environmental gradients. Specifically, a Principal Components Analyses (PCA) was used to transform the environmental variation into three principal components (PCs). We followed Fitzpatrick and Keller (2015), by centring but not scaling the transformed environmental variables, to retain the magnitude of the genomic importance among variables. The difference in allele frequencies between map cells was assigned to the first three PCs and partitioned into red/green/blue (RGB) colour palette, which were then mapped using the 'plotRGB' function of the *raster* R package. The resultant 'genomic turnover' maps indicate areas of genomic similarity by similar coloured map cells, and a change in allele frequencies by a change in colour. Individuals on either side of these turnover areas are presumed to have different demographic histories (if using neutral loci), or be under different selection pressures (if using outlier loci).

The GF turnover functions were also used to create 'genomic vulnerability' maps, which indicate areas where gene-environment relationships will be most disrupted under future climatic conditions (Bay et al., 2018; Fitzpatrick & Keller 2015). These maps were created by first transforming the future environmental variables in a similar manner as described above for the current day variables, and then calculating the Euclidean distance between the current and future genomic importance values for each map cell. Areas in which the Euclidean distances are high indicate populations that will experience the greatest impact from future environmental shifts, due to their alleles being less likely to match the climatic changes (Bay et al., 2018; Martins et al., 2018; Morgan et al., 2020). These genomic vulnerability maps are limited by the simplified gene-environment interactions used to identify the adaptive optima of alleles, but are still a novel and valuable tool to characterise relative vulnerability, without accounting for migration or multi-gene interactions allowing alleles to track climatic changes.

As only SNPs with a $R^2>0$ are included in the turnover functions and mapping analyses, the allele frequencies of the subset of SNPs retained in the GF models were visualised in PCAs created using *vegan* and *ggplot2* (Wickham, 2016) R packages. This was done to assess how well the SNPs in the GF models reflect patterns seen in the entire SNP datasets, which were previously used to assess neutral and outlier population structure (Nielsen et al., 2020b). To assess whether the different sets of environmental predictor variables lead to differences in the SDM and GF vulnerability outputs, additional GF models were run with the subset of uncorrelated environmental variables similarly used in the SDM models (referred to in the following section), as predictor variables. This exploratory analysis was conducted on the outlier SNP data, using RCP 4.5.

Species Distribution Models to predict future species ranges

Species distributions were projected into the future using correlative SDMs. These assume that environmental variables are the main determinant of species' distributions, and use correlations between environmental variation and contemporary species occurrence patterns to predict species distributions into new environmental space (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). Unlike GF models, SDMs cannot inherently account for collinearity between environmental predictor variables. Therefore, four environmental variables which are not correlated (Spearman's $R < 0.6$; Variance Inflation Factor < 10), but expected to be important drivers of rocky shore ecological niches, were used as predictor variables in the SDMs. Specifically, these were mean SST, mean SSS, maximum air temperature and minimum air temperature (all based on monthly averages). These variables were downloaded from the same databases, for the same GCMs, RCPs, and time points as those used in the GF models.

Species presences were composed of downloaded occurrences from the Global Biodiversity Information Facility (GBIF; GBIF, 2020) and the Ocean Biogeographic Information System (OBIS; OBIS, 2020) databases (which were pruned for data entry errors), as well as personal observations and sampling locations. An equal number of pseudo-absences (to presences) were randomly selected over five replicate runs using the *biomod2* R package (Bermejo et al., 2018). As an ensemble of multiple model types has been shown to increase overall accuracy (Araújo & New, 2007; Forester et al., 2013) an ensemble of six models (Flexible Discriminant Analysis [FDA]; Generalized Additive Model [GAM]; Generalized Boosting Model [GBM], Generalized Linear Model [GLM]; Multivariate Adaptive Regression Splines [MARS]; Random Forest [RF]) was created in *biomod2*. Models were run with default parameters, with the exception of using 1000 trees for GBM the 'mgcv' function for GAM. Data was randomly subset into 70% for calibration and 30% for validation, over ten evaluation runs and three permutations. Following best practice for marine SDMs (Bermejo et al., 2018; Bosch et al., 2018; Chefaoui et al., 2017) only models having Receiver Operating Characteristic (ROC; Fielding & Bell, 1997) greater than 0.8, and True Skill Statistic (TSS; Allouche et al., 2006) greater than 0.55 were retained in the ensemble per species.

To assess the extent to which the SDMs extend the relationships between current environmental conditions and species distributions into novel environmental conditions, we created two-dimensional convex hulls of the environmental space at five time points into the past and future. Specifically, we compared the environmental variation of the four predictor variables (mean SSS and SST, and minimum and maximum air temperature) at the present day, the Mid-Holocene (6 thousand years ago; kya), Last Glacial Maximum (21 kya), 2050, and 2070/2100 (Beaugrand et al., 2015). Historical environmental variables were downloaded from the MARSPEC database (Sbrocco, 2014), representing an average between CCSM4 and MIROC5 GCMs (as past environmental features were not available for HadGEM2-ES). Future environmental variables consisted of cell values averaged over the RCP 4.5 and 8.5 scenarios. The environmental values were extracted from 28 points, spaced 200km apart along the coastline, over the full extent of the SDMs (i.e. the extent used for *S. granularis*). Values were extracted for each time point, with the 28 points extrapolated to the -120m bathymetry line of the Last Glacial Maximum (Fig. S1, Appendix S1). Euclidean distances were calculated between time points, and two principal components from a PCA were used to maximize the amount of variation explained by the environmental variables. The global convex hull was mapped, including all five time points, onto which each time step's hull was mapped to compare the extent of environmental change across time periods (McWilliam et al., 2018).

Results

Genomic composition and vulnerability, and environmental drivers of these patterns

The R^2 weighted importance of environmental variables was higher in the outlier, compared to neutral SNPs, for all species (Fig. 3). Turnover in outlier SNP frequencies of the crab, *C. punctatus*, was strongly influenced by mean SSS, while those of the urchin, *P. angulosus*, and the limpet, *S. granularis*, were most strongly influenced by mean SST (Fig. 3). The cumulative importance plots (representing the GF turnover functions) also suggested that mean SSS and SST are important in driving the turnover of outlier frequencies of all species (Fig. S1-S3, Appendix S2). *Parechinus angulosus* and *S. granularis* showed congruent cumulative importance curves, with similar values of precipitation, and mean SSS and SST, leading to changes in outlier frequencies (Fig. S2-S3, Appendix S2).

The number of SNPs selected to create turnover functions differed between neutral and outlier SNPs per species, with 149, 112, and 340 neutral SNPs, and three, six, and 14 outlier SNPs having $R^2>0$ for *C. punctatus*, *P. angulosus*, and *S. granularis*, respectively (Table S1, Appendix S2). These subsets of loci generally reflected the genomic structuring seen in the entire SNP datasets, with the putative outlier loci showing more distinct east vs. west clustering than the neutral loci (Nielsen et al., 2020b; Fig. S4, Appendix S2). The patterns of genomic turnover, where map cells are coloured similarly if they portray similar allele frequencies, differed between the neutral and outlier loci, as well as across the three species. The neutral loci displayed higher genomic turnover along the eastern coast, while putative outlier loci showed higher turnover along the southwest coast (Fig. 4). The differences between genomic turnover between the outlier and neutral loci, calculated as Procrustes residuals, showed distinct areas of high differentiation in marker types between species (Fig. S5, Appendix S2). The highest discrepancies between neutral and outlier turnover were seen along the north-eastern coast for *C. punctatus* and the south coast for *P. angulosus* and *S. granularis* (Fig. S5, Appendix S2). The genomic turnover patterns of putative neutral and outlier loci generally followed the biogeographic breaks of the marine environment in the region (Fig. 2, Fig. 4).

When putative adaptive genomic composition was projected into the predicted environmental space of 2050, and 2070/2100, the results highlighted areas of increased genomic vulnerability where outlier allele frequencies will have to respond more rapidly to track future environmental changes (Fig. 5). Under the RCP 4.5 scenario, higher genomic vulnerability was found predominantly along the eastern South African coastline for *C. punctatus* (Fig. 5). In contrast, the west coast displayed higher genomic vulnerability for the other two species at both time points under RCP 4.5 (Fig. 5). Such species-specific patterns were also broadly found under the 'worst case' RCP 8.5 scenario, but with more of the coastline described as highly vulnerable at the 2070/2100 time point (Fig. S6, Appendix S2). These patterns were generally mirrored by the putatively neutral loci, with slight differences such as the *P. angulosus* west coast population being less vulnerable, and showing greater variation between RCPs 4.5 and 8.5 (Fig. S7, S8, Appendix S2). The models using the same four environmental variables as the SDMs demonstrated the same broad-scale patterns, but with *P. angulosus* showing high genomic vulnerability over a larger extent of the coastline, which is also pronounced by *S. granularis* at the 2070/2100 time point (Fig. S9, Appendix S2).

Forecasted species distributions and principal environmental features driving them

All individual model types resulted in relatively high ROC and TSS scores, and thus were included in the ensemble models for each species (Table S1, Appendix S1). Similar to the GF models, mean SSS was the most important predictor of *C. punctatus*, and mean SST was the most important predictor of *S. granularis* distributions in the SDMs (Fig. S2, Appendix S1). For *P. angulosus*, minimum air temperature and mean SSS were the important predictor variables in the SDMs (Fig. S2, Appendix S1). The species distribution models under RCP 4.5 showed distinct distributional changes both between species, and within a species across time steps (Fig. 6). At the 2050 projection, *C. punctatus* exhibited an increase in habitat suitability along the west coast, *P. angulosus* showed a decrease in suitability along the east and western coasts, and *S. granularis* showed a slight reduction in suitability along the range edges (Fig. 6). These changes were slightly more pronounced in the RCP 4.5 2070/2100 projections, with most of the southern African coastline projected as habitable for *C. punctatus*, and *S. granularis* and *P. angulosus* being restricted to the south and western southern African coasts (Fig. 6). Similar distributional patterns were projected under RCP 8.5, but with habitat suitability being lower overall for all three species, especially for *P. angulosus* and *S. granularis* at the 2070/2100 time point (Fig. S3, Appendix S1).

The convex hulls of the environmental space showed that going further into the past and/or future lead to greater deviations from the reference environmental space used in the SDMs, but did not significantly differ from the present-day space, as all of them contained the centroid of the hull (Fig. 7). Therefore, as expected, the models in 2070/2100 are potentially less certain than those for 2050. However, overall the model environmental space did not substantially change from the current environmental space, validating their use.

Discussion

This study provides novel insights into assessing the vulnerability of marine species to global change, which we found varies both within and between species. Here, SDMs predicted species-specific range shifts, yet the modelled predictions did not capture the high genomic vulnerability that some populations will likely experience within these species level changes. Thus, species level predictions alone may misrepresent the vulnerability of a species to climate change, by disregarding an individual population's potential adaptive capacity to novel environments. We also found that outputs from the GF models resulted in more variation between different RCPs and timeframes than the SDMs, suggesting that gene-environment relationships may be more sensitive to differences in environmental shifts. As such, including these relationships can potentially offer more fine-scale projections in species vulnerability assessments. The results from both model types also portrayed how multiple, species-specific, variables can be important drivers of biological patterns at species and genomic levels, corroborating calls for studies predicting marine species' responses to future climatic change to include a multitude of variables in addition to sea temperature (McHenry et al., 2019). Additionally, while the genomic turnover patterns varied among species, and between putative neutral and adaptive markers, they broadly correlated with known biogeographic breaks. In a South African context, these breaks may be useful proxies for intraspecific evolutionary distinctness (Teske et al., 2011), but further work is needed to understand whether and how shifts in biogeographic breaks due to global change will influence species and population dynamics.

As marine conservation strategies aimed to maximise resilience increasingly include actions to both promote adaptation and mitigate the effects of climate change (Rilov et al., 2020; Wilson et al., 2020), it is important to understand how vulnerability differs between metrics pertaining to species and populations. This study demonstrates how assessments of vulnerability differ between ecological processes shaping species distributions and evolutionary processes shaping population dynamics. The results indicate that resilience hotspots may vary depending on the vulnerability metric and/or species assessed, and provide a basis for future investigations into the complex ecological-genomic interactions within marine environments.

Patterns of genomic composition between markers and species

Broadly, we found differences in spatial genomic vulnerability among three co-distributed coastal species, as well as between putatively neutral and outlier markers within each species (Fig. 5; Fig. S6-S8, Appendix S2). This is expected, as vulnerability to climate change has been shown to be highly species-specific (Román-Palacios & Wiens, 2020; Sunday et al., 2015). In addition, statistical outlier loci often show distinct patterns of genomic variation compared to putative neutral loci datasets (Grummer et al., 2019; Phair et al., 2019). Yet, despite the species differing in ecology and life history, all species display genomic turnover (shown by the changes of colour in Fig. 4) that relates to the biogeographic breaks in the region (Fig. 2). These findings suggest that the environmental features shaping biogeography may extend to the molecular level of biodiversity patterns. For example, Stanley et al. (2018) found that genomic patterns corresponded to ecoregion delineations for five marine species with varying distributions and life histories in the northwest Atlantic. However, our findings provide a deeper level of insight by delineating turnover patterns between putatively neutral and outlier loci, in which we found that both data types roughly follow biogeographic breaks. Broadly, the findings demonstrate how environmental gradients, and the evolutionary processes they enact on species, can lead to intraspecific genomic clusters which have distinct evolutionary trajectories compared to the species as a whole (Prates et al., 2018; Razgour et al., 2018). Identifying these genomic clusters can be especially powerful when combined across taxa, which can indicate biogeographically significant units for conservation (Quiroga et al., 2019).

Environmental drivers of species and genomic level composition

Although the results showed similar genomic turnover patterns across species, the environmental variables driving these patterns were species-specific. Further, our work suggests that the principal environmental variables in genomic turnover functions differ between putatively neutral and adaptive loci. Similar to other work on these species (Nielsen et al., 2020b), both the GF and SDM analyses highlighted the importance of SSS for the crab, and SST for the limpet. Sea-surface temperature is a prevailing determinant of marine invertebrate distributions globally (Bosch et al., 2018), which is reflected here in the limpet distribution, and by the limpet and urchin genomic compositions. In contrast, the distribution of the crab was best explained by salinity, which was more unexpected as this species also inhabits estuarine environments, and has a wide salinity tolerance (Boltt & Heeg, 1975).

However, the importance of salinity in the crab's distribution could be driven by larval and juvenile life history stages, as salinity is a key parameter in larval development of decapod crustaceans (Anger, 2003). This notion is further supported by salinity proving to have a higher effect on the osmoregulatory abilities of juvenile, compared to adult, *C. punctatus* individuals (Winch & Hodgson, 2007). The urchin distribution was found to be mainly driven by SSS and minimum temperature in the SDMs (Fig. S2, Appendix S1) and by SST and range in precipitation in the GF models (Fig. 3; Fig. S2, Appendix S2). This mirrors findings of Nielsen et al. (2020b), who found that the urchin showed selection signals from a combination of variables, compared to the strong selection patterns from solely SSS or SST, shown by the crab and limpet, respectively. We expected the urchin to be the least influenced by atmospheric variables, as it has the lowest rocky shore zonation of the three species, and as many studies indicate that sea temperature is highly important in urchin behaviour and physiology (Branco et al., 2013; Brothers & McClintock, 2015; Delorme et al., 2020; Pérez-Portela et al., 2020; Zhang et al., 2017). Our finding of air temperature being more important in the urchin SDMs could be driven by multiple factors, such as this environmental feature being an important driver of other species in which the urchin is ecologically linked to, or minimum temperature being highly correlated to an environmental variable directly influencing the urchin's biology but not included in the model, or due to biases from the spatial resolution and occurrence points (Smith & Santos, 2020). The urchin was also found to be strongly influenced by SSS in the SDMs, which could be due to changes in salinity being an important driver at multiple life history stages, as the larval development of urchin species has been shown to be highly sensitive to changes in salinity (Carballeira et al., 2011; Mak & Chan, 2018). Bosch et al. (2018) found that globally, SST and SSS have a strong importance in describing echinoderm, mollusc and arthropod distributions, which suggests that both of these variables should being included in SDMs predicting marine invertebrate species' responses to global change. Ultimately, further research into the physiological, behavioural and ecological responses of marine species, across different life stages is crucial for better interpreting future patterns of species in changing environments.

In the genomic turnover functions, SST appeared to be the most important predictor for both the urchin and limpet (Fig. 3.; Fig. S2, S3, Appendix S2), yet the resultant genomic vulnerability patterns differed between the two species, with the limpet having higher genomic vulnerability across southern Africa, in both neutral and outlier SNPs (Fig. 5; Fig. S6-S8, Appendix S2). Similarly, although the limpet and urchin have congruous contemporary distributions, the predicted habitat suitability of the two species differed into the future (Fig. 6). Similar discrepancies in forecasted distributions were found between two co-distributed *Anolis* lizard species, which the authors attribute to species-specific ecological and demographic constraints (Prates et al., 2016). Therefore, even though temperature has been shown to be a principal driver of biological patterns in marine systems (Bosch et al., 2018), individual species responses to fluctuations in temperature are likely to differ based on their ecology and demographic histories (Nielsen et al., 2020b; Sunday et al., 2015).

While species- or gene-environment association analyses are vital tools to predict species' responses to forecasted climatic change, they solely encapsulate correlations with the environment, disregarding integral biological processes and interactions. The inclusion of the latter may thus lead to further interspecific differences in vulnerability, particularly with the emergence of novel communities in response to climatic change (Catullo et al., 2015). Further work such as mechanistic and joint species distribution models, physiological measurements, and adaptive and demographic models are essential to fully understand each species' responses to global change (Bush et al., 2016; Rilov et al., 2019). As a whole, our results stress the importance of comparative species distribution and seascape genomic analyses, which are an essential step towards elucidating ecosystem level resilience to global change.

Species and genomic level forecasts identify distinct vulnerability hotspots

The SDM and GF models offered distinct insights into areas where the study species will be at increased risk to future climatic change. From the SDMs, the limpet, and especially the urchin, showed range reductions, with only the western and southern coastline remaining habitable into the future (Fig. 6; Fig. S3, Appendix S1). This region is characterised by the Benguela upwelling ecoregion, which is experiencing a cooling trend due to increased upwelling, compared to the Agulhas current on the east coast, which is predicted to follow global warming trends (Rouault et al., 2010). The Benguela upwelling system may thus act as an important climatic refuge for other cool-temperate marine species in the region (Greenstein & Pandolfi, 2008; Riegl & Piller, 2003). In contrast, for the crab, the SDMs predicted that exposure to unfavourable environmental conditions will be far less pronounced than for the other two predominantly cool-temperate species. Specifically, it is forecasted that *C. punctatus* will expand its range both up the west and east southern African coast, as these marine environments become warmer and more saline (Fig. 6; Fig. S3, Appendix S1). However, the GCMs used here predict ocean warming along the entire South African coastline, and thus do not account for the recent local cooling trend and increased upwelling within the Benguela current on the west coast (Rouault et al., 2010). The crab's range expansion might be further impeded into the north-eastern Delagoa bioregion, as the species showed high levels of genomic vulnerability from the GF models in this area (Fig. 5).

The results here also contradict the general assumption of species with narrow range sizes being more vulnerable to climate change and local extirpation (Purvis et al., 2000). We show that the crab, which has the smallest contemporary distribution, is predicted to be the least negatively affected by future environmental change based on the SDMs (Fig. 6; Fig. S3 Appendix S1). The SDMs also showed the least variation in habitat suitability between RCPs for the crab, while RCP 8.5 outputs displayed more severe habitat loss for the limpet and the urchin, especially at the 2070/2100 time point (Fig. 6; Fig. S3, Appendix S1). Confidence in SDM outputs has been shown to vary depending on the number different RCPs, GCMs, and SDMs included (Thuiller et al., 2019), as well as the extent that the models predict into new geographic or environmental space; i.e. their transferability (Yates et al., 2018). We assessed the transferability of forecasted SDMs with convex hulls of the modelled environmental space, showing that predictive ability decreases further into the future, but does not drastically differ from environmental variability into the past (Fig. 7).

The SDMs used here also assumed that there is available habitat within the entire region, that species cannot respond by adaptation and plasticity, and that environmental changes act on adult and larval stages equally, all leading to uncertainty in our predictions (Reusch, 2014). Furthermore, even though the SDMs identified the crab as a climate change 'winner', due to its broadly warm-temperate, rather than cool-temperate range, its argued that warm-adapted coastal species are actually the most at risk to climate change due to their upper thermal limits being closer to their thermal optima (Somero, 2010). This is supported by the crab population in the warm-temperate region of South Africa having higher genomic vulnerability into the future (Fig. 5), meaning potentially warm adapted individuals might not be able to cope with further warming. It should also be noted that predicted species distributional changes do not account for behavioural mechanisms, such as actively selecting microhabitats, to remain within their thermal optima (Chapperon et al., 2017; Seabra et al., 2011). While our results showed clear differences in predicted species responses to forecasted climatic changes, further analyses are ideally needed to assess the uncertainties in the SDMs, such as incorporating physiological tolerance (Franco et al., 2018), habitat condition (Hattab et al., 2014), and species interactions (Fulton, 2011) into the models.

In addition to predicted species distributions, we also pinpointed areas of high genomic vulnerability, in which populations will likely have to drastically adapt to track future environmental changes (Fitzpatrick & Keller, 2015). As expected, the results showed a mismatch between species and population level sensitivity to future environmental change. For the crab, populations inhabiting the east coast were estimated to be highly sensitive to climatic changes based on their genomic vulnerability, yet this area was predicted to be highly stable based on the SDMs (Fig. 5, 6). Further, the west coast populations of both the urchin and limpet were predicted to have higher vulnerability to future environmental change, yet this region was also predicted to remain more habitable than the east coast within the SDMs (Fig. 5, 6). These patterns were broadly mirrored by those under RCP 8.5 (Fig. S6, Appendix S2), but with more of the coastline being highly vulnerable for all species, especially in 2070/2100. Furthermore, the GF outputs were similar between those run using all eight environmental predictor variables or using the four same environmental predictor variables as in the SDMs, but with high genomic vulnerability extending over a larger area of the coastline further into the future with the smaller set of variables (Fig. S9, Appendix S2). Most studies to date have not considered multiple time points and RCPs when assessing genomic vulnerability, but the few that do (e.g. Jia et al., 2020; Morgan et al., 2020), as well as this study, suggest that increasing RCPs and timeframes leads to similar spatial patterns, but with overall increased vulnerability. As we did find differences in outcomes between species, environmental variables, and RCPs included in the GF models, it is important that these types of genomic vulnerability analyses follow the general 'best practices' of SDMs, by including multiple model inputs to better asses their uncertainty (Robinson et al., 2017; Thuiller et al., 2019).

Even though there were only a few outlier loci from which the genomic vulnerability measures were derived, similar patterns were generally shown by the larger subsets of putatively neutral loci (Fig. S7, S8, Appendix S2), indicating that putatively neutral and adaptive loci may have similar gene-environment relationships, but to different extents. For example, Martins et al. (2018) also found similar spatial patterns of genomic vulnerability between all loci or solely environmental-associated loci, yet the latter of the two datasets displayed larger offset values. Our findings support the concept that local adaptation along environmental clines is not only shaped by selection, but also by neutral processes such as demographic history, contemporary gene flow, and standing genomic variation (Cayuela et al., 2020; Nadeau et al., 2016).

Overall, the results suggest that climatic exposure (i.e. the extent of environmental change experienced by a species) may not directly relate to climatic sensitivity and adaptive potential (i.e. how well equipped species are to respond to environmental change; Dawson et al., 2011). For example, even though the west coast populations of the limpet and urchin are predicted to remain within each species' known environmental space, many of the cold adapted individuals in these populations may not be genetically equipped to adapt to warming temperatures (if warming does indeed happen here). Alternatively, the east coast populations of the crab may not be able withstand temperature or salinity changes due to genomic, rather than ecological, constraints. Changes to these gene-environment associations may lead to changes in species abundances, consequently altering community composition, further impacting species distributions (Harley et al., 2006). However, further testing is needed, such as with whole genome sequencing and/or transplant and common garden experiments, to validate the assumption that the correlations between allele frequencies and environmental variables reflect patterns of local adaptation and fitness (Fitzpatrick et al., 2018). Also, this study was limited to relatively small SNP datasets, using RAD-seq and non-model marine species, and as such, greater inferences can be made using more advanced genomic techniques on species with available reference genomes (Benjelloun et al., 2019; Manel et al., 2016). Furthermore, measures of genomic vulnerability cannot account for shifts in allele frequencies due to selection, genetic drift, or gene flow, and therefore may overestimate (Exposito-Alonso et al., 2018) or underestimate (Crisci et al., 2017) vulnerability. It should also be noted that the study species are expected to have relatively high adaptive capacity, as they have large effective population sizes, overlapping generations, and dispersive reproductive modes, and thus spatial vulnerability patterns should also be assessed in species with traits making them sensitive to change (Bennett et al., 2019; Catullo et al., 2015).

Potential implications for conservation

Climatic refuges identified from SDMs are increasingly informing conservation planning to promote species resilience (Morelli et al., 2016; Wilson et al., 2020). We show here that genomic and other population level measures of vulnerability are also crucial to predict species' responses to climate change. Because both SDMs and GF model outputs are limited by various levels of uncertainty, using them in combination and highlighting areas of overlap can potentially lead to more robust inferences of future climatic refuges, especially when combined across multiple species. For example, the results here suggest that the southern coast of South Africa is the least vulnerable to future change across models and species, echoing local predictions of southern African endemic coastal species being squeezed southwards by the cooling west coast and warming east coast (Blamey et al., 2015; Whitfield et al., 2016).

Alternatively, due to the differences in environmental space restricting species and genomic composition found here, and presumed differences in how species and genes will respond to environmental change, prioritizing areas over an array of climatic velocities may be the best way to ensure species persistence. This 'portfolio approach' of prioritizing a range of current and future suitable habitats and environmental conditions is key to ensure that adapted populations can actively or passively enhance the gene pools of those populations less likely to track future environmental change (Beyer et al., 2018; Matz et al., 2020). While further work is needed to fully describe the adaptive capacity of coastal marine systems in our study region and elsewhere (Munday et al., 2013), this study is an essential step in understanding marine species' sensitivity to global change across biological scales, and offers a unique framework to further understand species resilience to changes in biological-environmental interactions.

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Figures

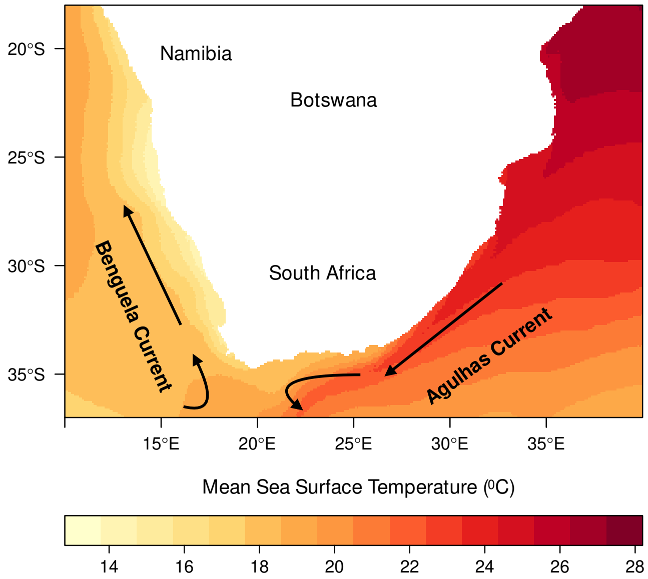

Figure 1- Sea surface temperatures (averaged over 2000–2014 and from Bio-Oracle2.0; Assis et al., 2018), increasing from yellow to red, and major ocean currents within the study region.

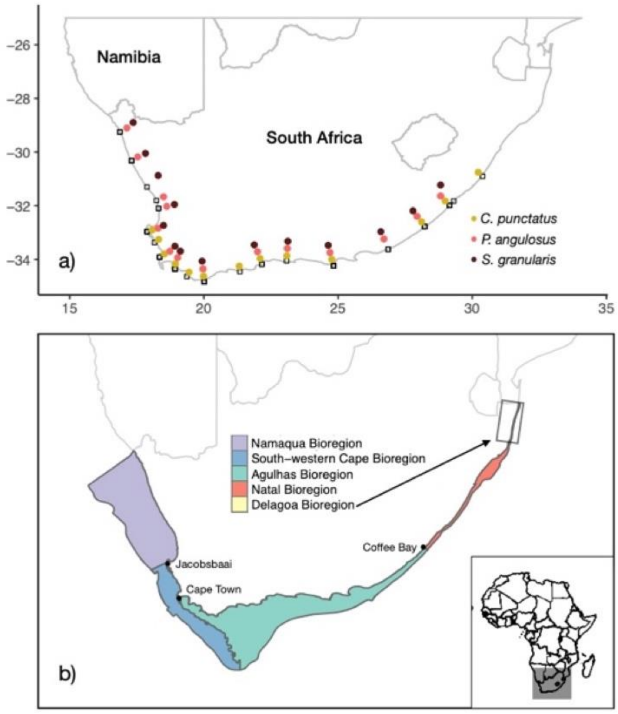

Figure 2- Samples sites from which genomic data was obtained for *C. punctatus*, *P. angulosus*, and *S. granularis* (a), as well as the bioregions obtained from van der Bank et al., (2019), with the Delagoa Bioregion indicated in the box for clarity (b).

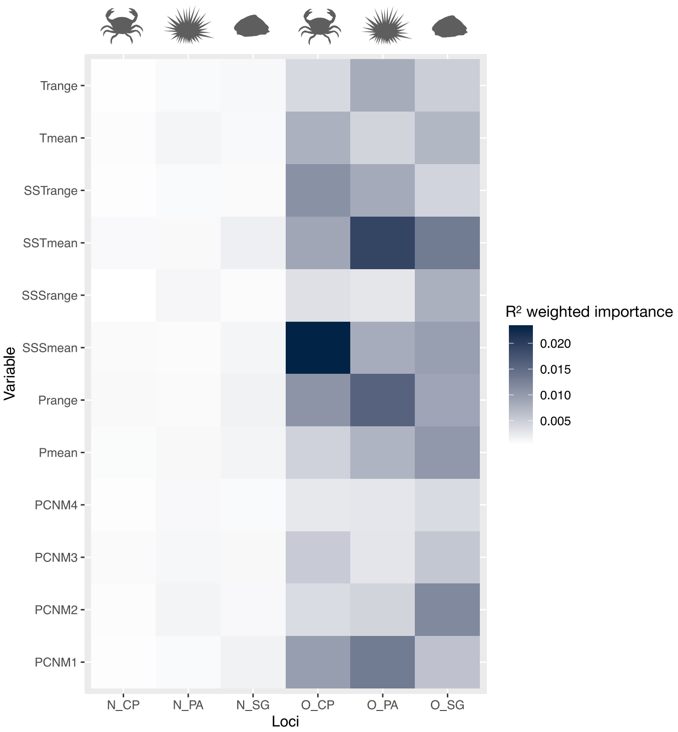

Figure 3- The relative importance of each environmental predictor variable in describing the turnover in allele frequencies from the Gradient Forest models based on either neutral (N_*) or outlier (O_*) loci for *C. punctatus* (*_CP), *P. angulosus* (*_PA) and *S. granularis* (*_SG). Darker shaded squares represent higher importance of predictor variables per genomic dataset. Predictor variables shown here include: range in air temperature (Trange), mean air temperature (Tmean), range in sea surface temperature (SSTrange), mean sea surface temperature (SSTmean), range in sea surface salinity (SSSrange), mean sea surface salinity (SSSmean), range in precipitation (Prange), mean precipitation (Pmean), and four principal coordinates of neighbour matrices (PCNMs).

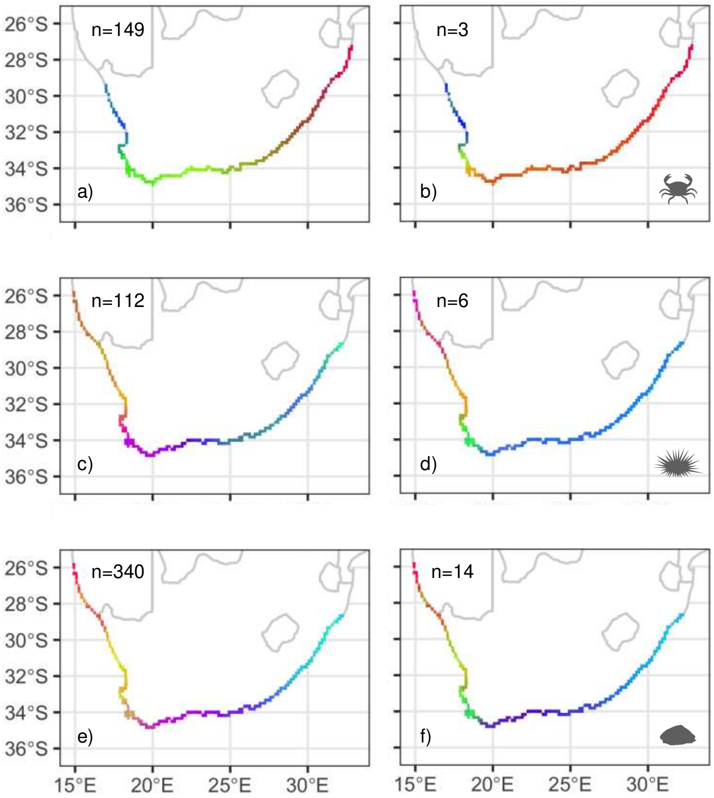

Figure 4- The composition of genomic turnover shown in geographic space, in which the first three principal components of the Gradient Forest transformation of allele frequencies are partitioned into the red, green, and blue colour palette and each palette is overlaid, creating the colours seen on the maps. The colours are arbitrary, but similar coloured map cells indicate similar allele frequencies in either putatively neutral (a, c, e) or outlier (b, d, f) loci for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Only alleles with a $R^2>0$ were included in the Gradient Forest transformations (number in the top left corner).

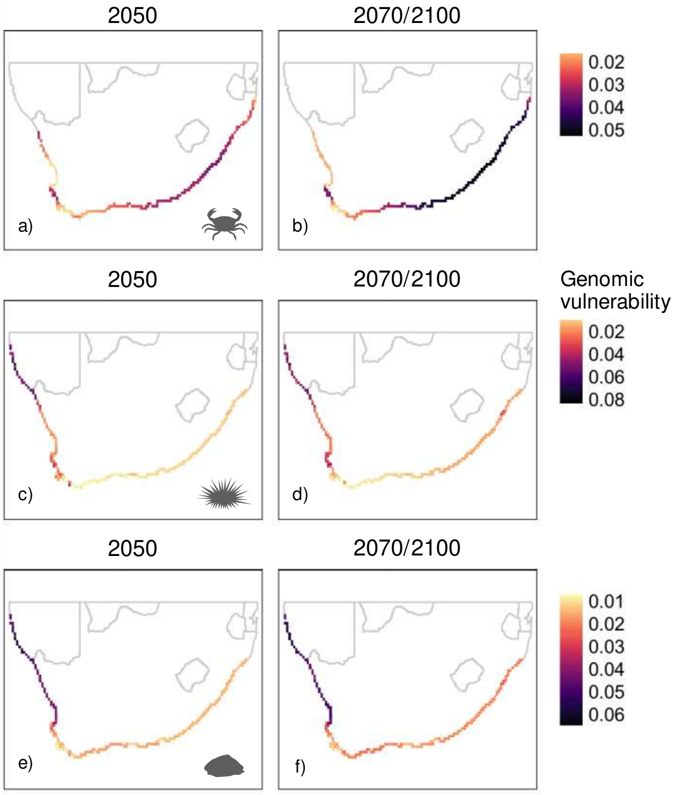

Figure 5- Spatial patterns of outlier genomic vulnerability, calculated as Euclidean distance between current and future genetic spaces, shown for RCP 4.5, for 2050 (a, c, e), and 2070/2100 (b, d, f; 2070 for landscape, and 2100 for seascape variables), for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Areas with darker coloration indicate areas of high vulnerability, where genomic composition will have to change the most to track environmental change.

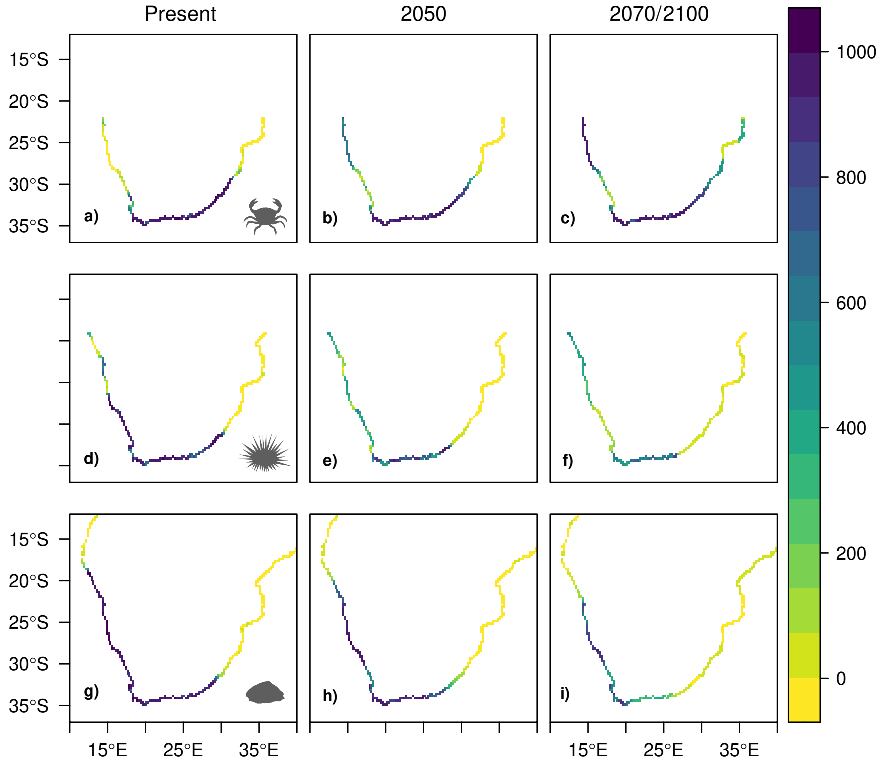

Figure 6 - Habitat suitability (ranging from zero, where species will likely be absent, to 1000, where species are most likely to be present) is shown for present day (a, d, g), and in the future under the intermediate RCP 4.5 scenario at 2050 (b, e, h), and a combination of 2070 for the two terrestrial variables and 2100 for the two seascape variables (c, f, i), for *C. punctatus* (a-c), *P. angulosus* (d-f), and *S. granularis* (g-i). Darker shaded regions represent higher habitat suitability.

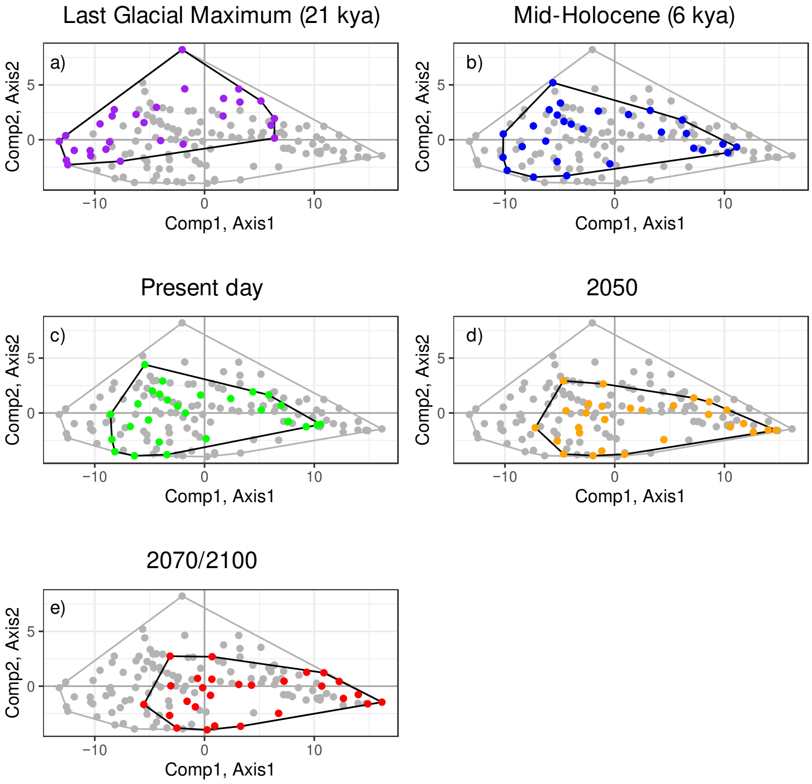

Figure 7- Environmental variation within the species distribution models, shown in two-dimensional space, with the global environmental space across all five time points shown in grey, and the environmental space pertaining to each time period overlaid in colour. The Present day (c), as well as two past time points: Last Glacial Maximum (a), Mid-Holocene (b); and two future time points: 2050 (e), 2070/2100 (f; 2070 for terrestrial layers, and 2100 for oceanic layers) are shown.

Supporting information for "Distinct inter- and intra-specific vulnerability of coastal marine species to global change" – Additional information pertaining to individual species distribution models, convex hulls, and gradient forest models.

Appendix S1- Individual and ensemble model scores and the variable importance of each variable in SDMs per species are shown. The points used to generate change in overall environmental space over the SDMs for the convex hulls are also shown.

Table S1. Individual and ensemble model scores, shown as the average Receiver Operating Characteristic (ROC) and True Skill Statistic (TSS) per individual model, namely: Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and Random Forest (RF).

	C. punctatus		***P. angulosus***		***S. granularis***	
Model	**ROC**	**TSS**	**ROC**	**TSS**	**ROC**	**TSS**
FDA	0.76	0.47	0.89	0.63	0.87	0.64
GLM	0.77	0.50	0.90	0.64	0.86	0.64
GAM	0.77	0.50	0.90	0.65	0.89	0.71
GBM	0.77	0.48	0.92	0.69	0.93	0.71
RF	0.76	0.49	0.93	0.73	0.96	0.77
MARS	0.76	0.46	0.89	0.64	0.87	0.66
Ensemble	0.86	0.58	0.96	0.79	0.96	0.78

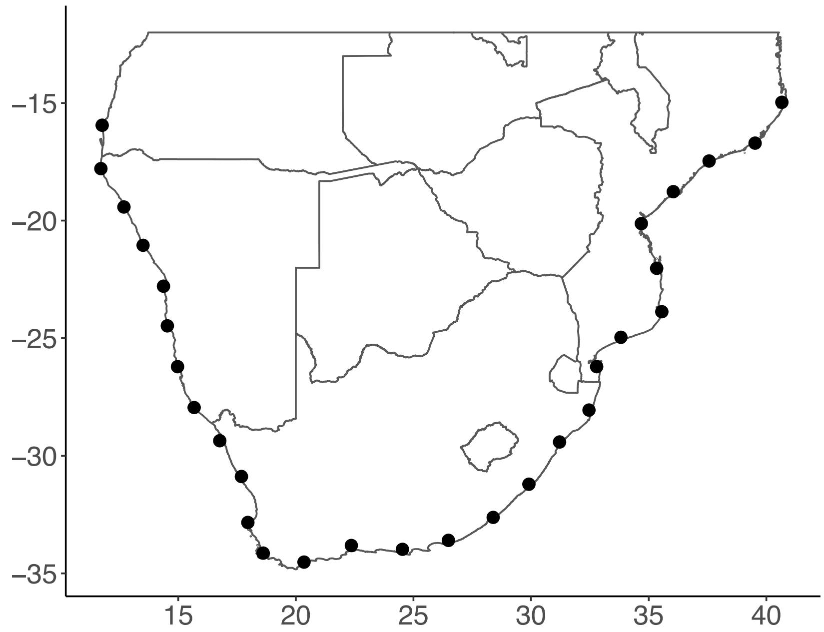

Figure S1. The localities from which environmental data was extracted to create two-dimensional environmental hulls across time points.

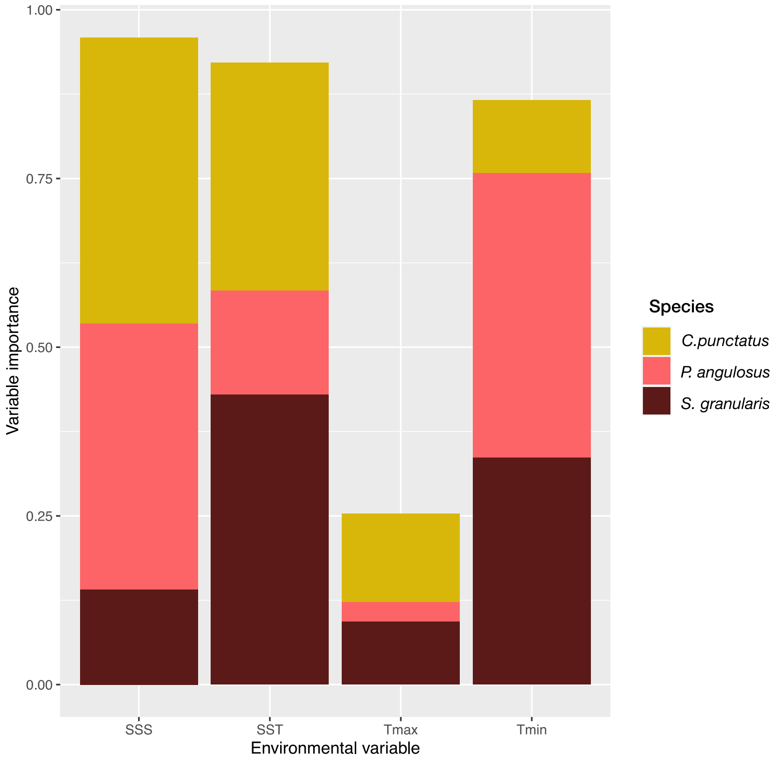

Figure S2. The importance of each environmental variables in describing the distributions of *C. punctatus*, *P. angulosus*, and *S. granularis* within the species distribution model ensembles. The four environmental variables are as follows: mean sea-surface salinity (SSS), mean sea-surface temperature (SST), maximum air temperature (Tmax), and minimum air temperature (Tmin).

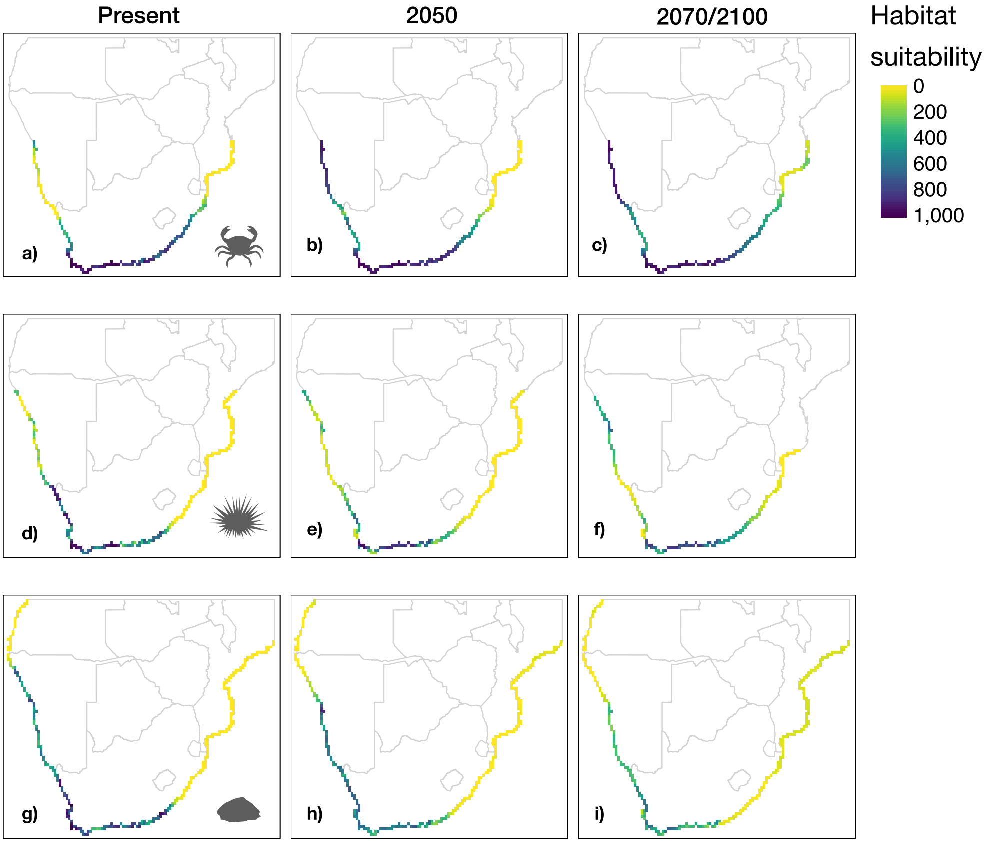

Figure S3. Habitat suitability (ranging from zero, where species will likely be absent, to 1000, where species are most likely to be present) is shown for present day (a, d, g), in the future under the 'worst case' RCP 8.5 scenario at 2050 (b, e, h), and a combination of 2070 for the two terrestrial variables and 2100 for the two seascape variables (c, f, i), for *C. punctatus* (a-c), *P. angulosus* (d-f), and *S. granularis* (g-i). Darker shaded regions represent higher habitat suitability.

Appendix S2- The number of loci and mean R^2 of those loci in the Gradient Forest (GF) models, cumulative importance curve outputs from GF models, Principal Components Analyses of allele frequencies from the subset of SNPs included in the GF models, and difference in spatial genomic turnover patterns between putatively neutral and outlier SNPs are shown. Additionally, the genomic vulnerability of outlier SNPs under RCP 8.5, and neutral SNPs at RCPs 4.5 and 8.5, and vulnerability of outlier SNPs under RCP 4.5 predicted from the four environmental variables as in the species distribution models are also shown per species.

Table S1. The number (#) of loci which had a R^2 value greater than (>) zero, and the mean R^2 values from the Gradient Forest models run on putatively neutral, or statistically outlier allele datasets, for *C. punctatus*, *P. angulosus*, and *S. granularis*.

	C. punctatus	*P. angulosus*	*S. granularis*
# of neutral loci with $R^2 > 0$	149	111	340
# of outlier loci with $R^2 > 0$	3	6	14
Mean R^2 of neutral loci	0.154	0.162	0.206
Mean R^2 of outlier loci	0.283	0.442	0.390

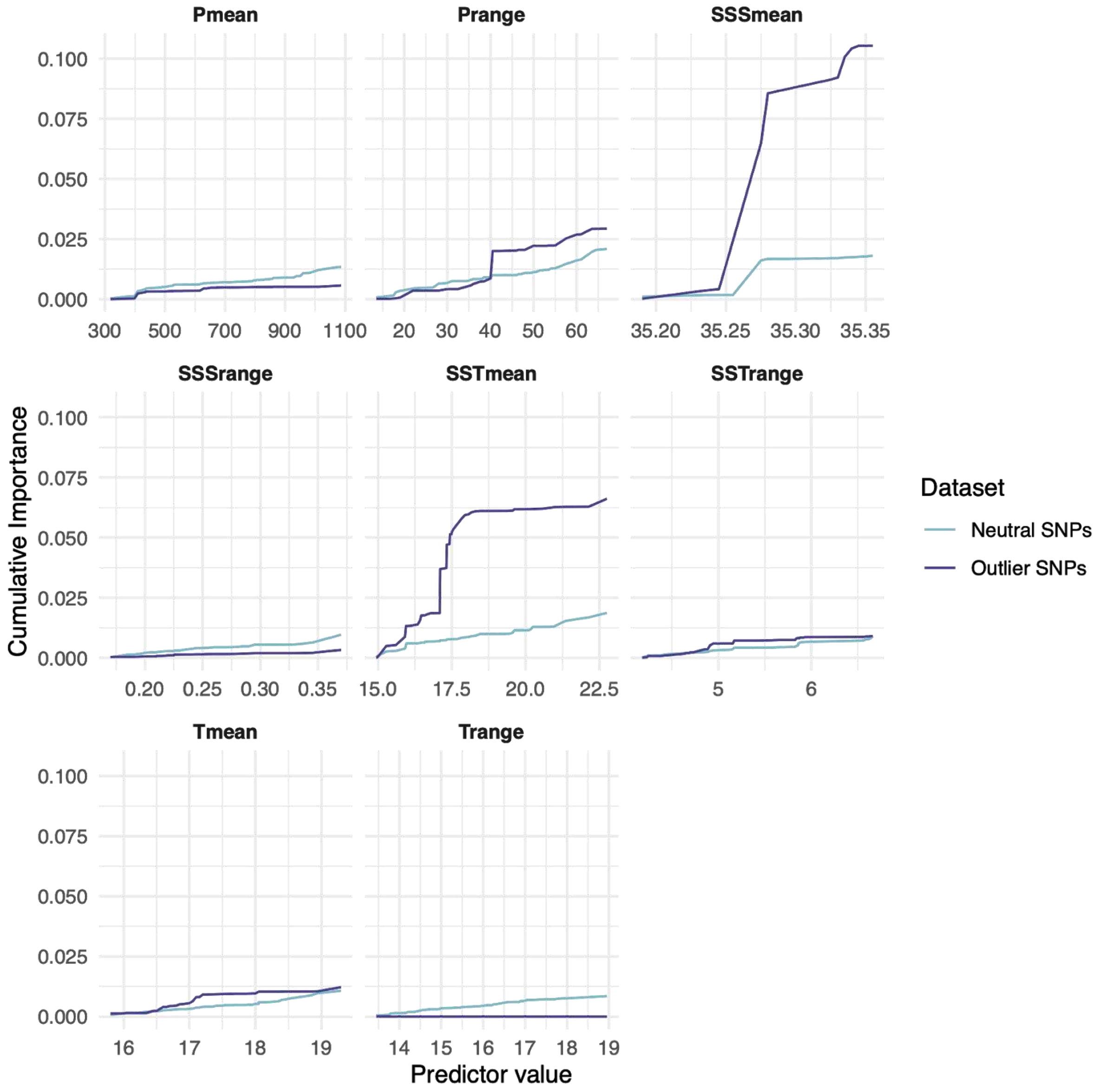

Figure S1. Cumulative importance curves based on the turnover functions from each environmental variable in the Gradient Forest models for the crab, *C. punctatus*. The curve shape indicates the rate of change in allele frequencies along the environmental gradient, and the maximum height indicates the total turnover in allele frequencies. Curves are shown for both neutral and outlier datasets, and the number of loci within these datasets is shown in Table S1. Predictor variables shown here include: range in air temperature (Trange), mean air temperature (Tmean), range in sea surface temperature (SSTrange), mean sea surface temperature (SSTmean), range in sea surface salinity (SSSrange), mean sea surface salinity (SSSmean), range in precipitation (Prange), and mean precipitation (Pmean).

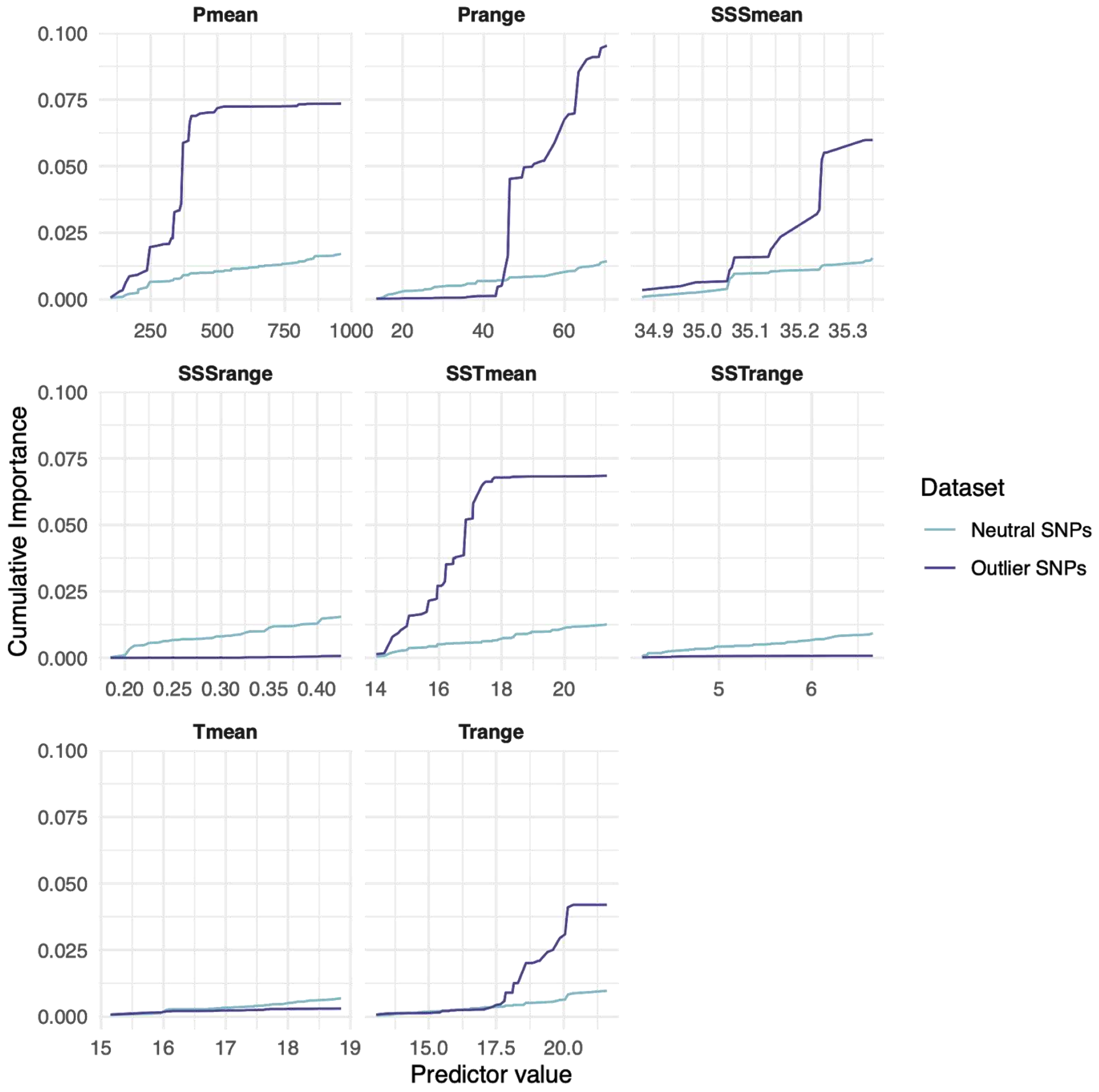

Figure S2. Cumulative importance curves based on the turnover functions from each environmental variable in the Gradient Forest models for the urchin, *P. angulosus*. The curve shape indicates the rate of change in allele frequencies along the environmental gradient, and the maximum height indicates the total turnover in allele frequencies. Curves are shown for both neutral and outlier datasets, and the number of loci within these datasets is shown in Table S1. Predictor variables shown here include: range in air temperature (Trange), mean air temperature (Tmean), range in sea surface temperature (SSTrange), mean sea surface temperature (SSTmean), range in sea surface salinity (SSSrange), mean sea surface salinity (SSSmean), range in precipitation (Prange), and mean precipitation (Pmean).

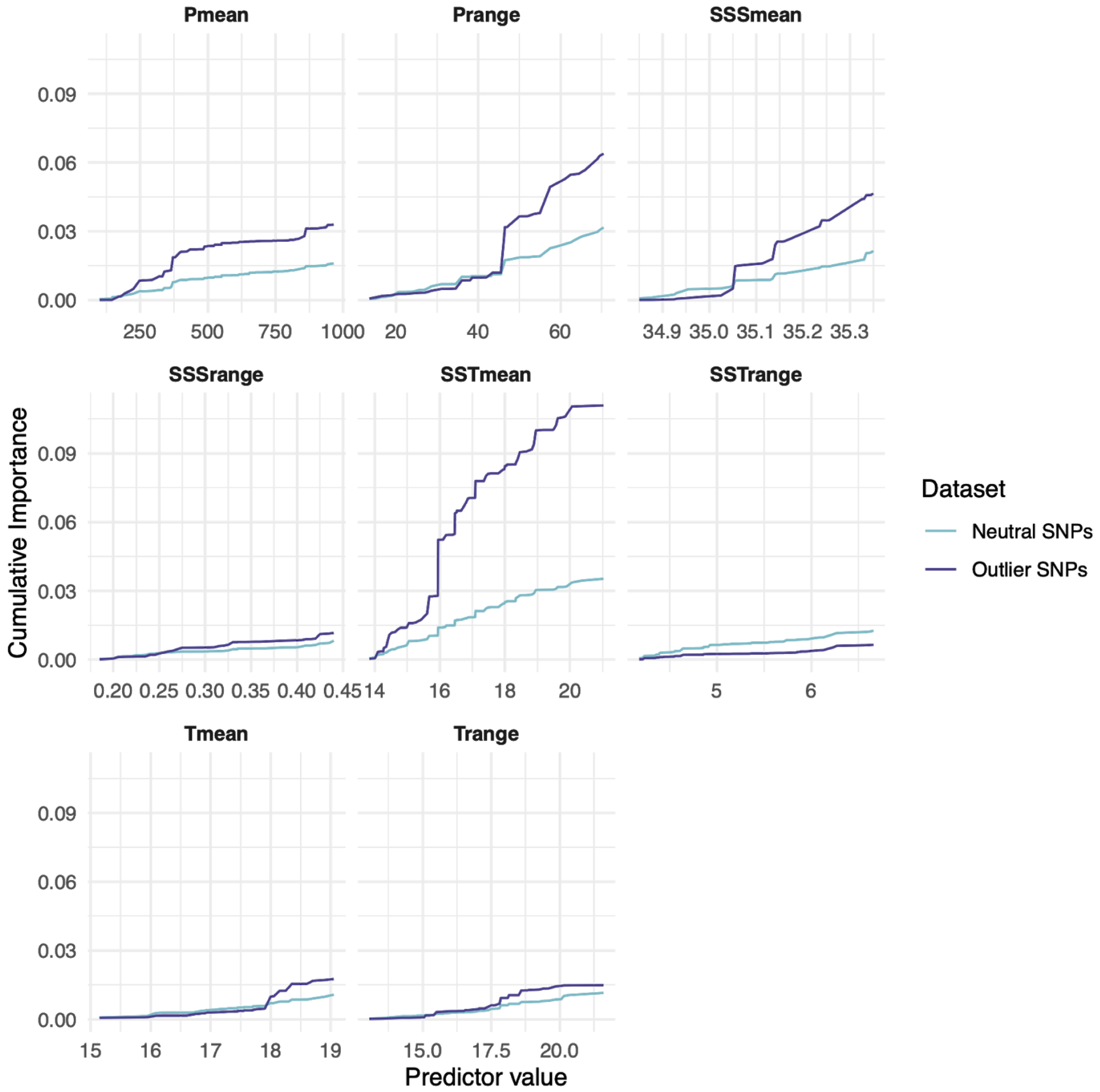

Figure S3. Cumulative importance curves based on the turnover functions from each environmental variable in the Gradient Forest models for the limpet, *S. granularis*. The curve shape indicates the rate of change in allele frequencies along the environmental gradient, and the maximum height indicates the total turnover in allele frequencies. Curves are shown for both neutral and outlier datasets, and the number of loci within these datasets is shown in Table S1. Predictor variables shown here include: range in air temperature (Trange), mean air temperature (Tmean), range in sea surface temperature (SSTrange), mean sea surface temperature (SSTmean), range in sea surface salinity (SSSrange), mean sea surface salinity (SSSmean), range in precipitation (Prange), and mean precipitation (Pmean).

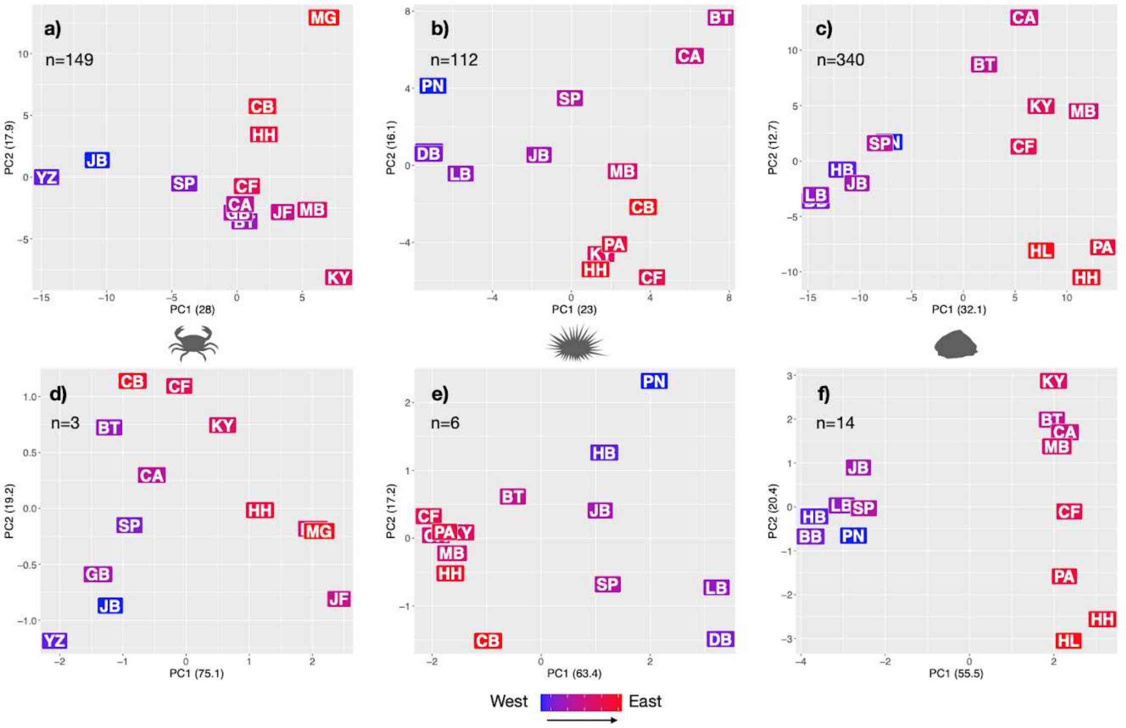

Figure S4. Genomic differentiation shown by Principal Components Analyses (PCAs) of allele frequencies, pertaining to either the neutral (a, b, c) or outlier (d, e, f) SNPs used in the Gradient Forest turnover functions (number of loci per dataset is indicated on plots), shown for *C. punctatus* (a, d), *P. angulosus* (b, e), and *S. granularis* (c, f).

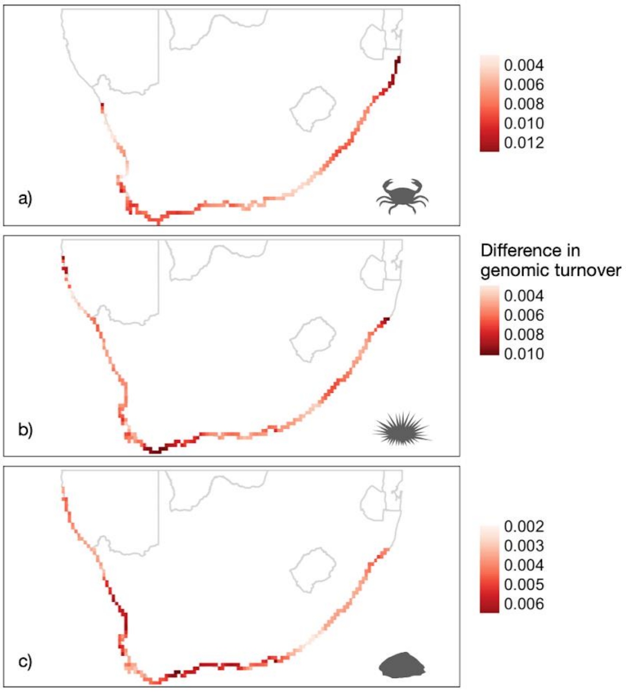

Figure S5. Differences in genomic turnover composition in geographic space between neutral and outlier SNP frequencies, based on Procrustes residuals. Differences between the two markers are shown for *C. punctatus* (a), *P. angulosus* (b), and *S. granularis* (c), with darker red areas indicating a larger distinction between the two molecular datasets.

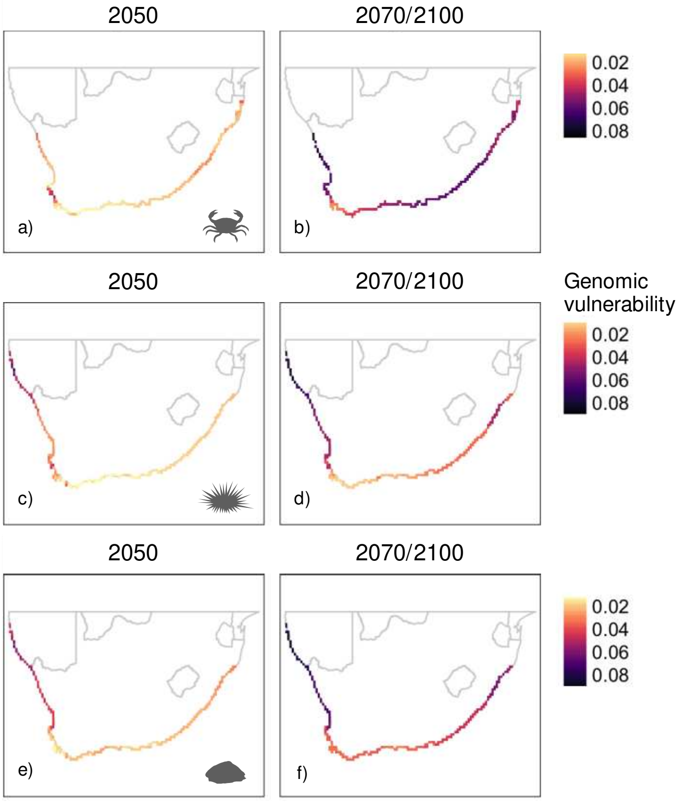

Figure S6. Genomic vulnerability patterns of outlier SNPs, calculated as Euclidean distance between current and future genetic spaces, under the RCP 8.5 scenario for 2050 (a, c, e), and 2070/2100 (b, d, f; 2070 for landscape features, 2100 for seascape features), for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Darker shaded regions represent areas of higher genomic vulnerability, where genomic composition will be altered the most to track environmental changes.

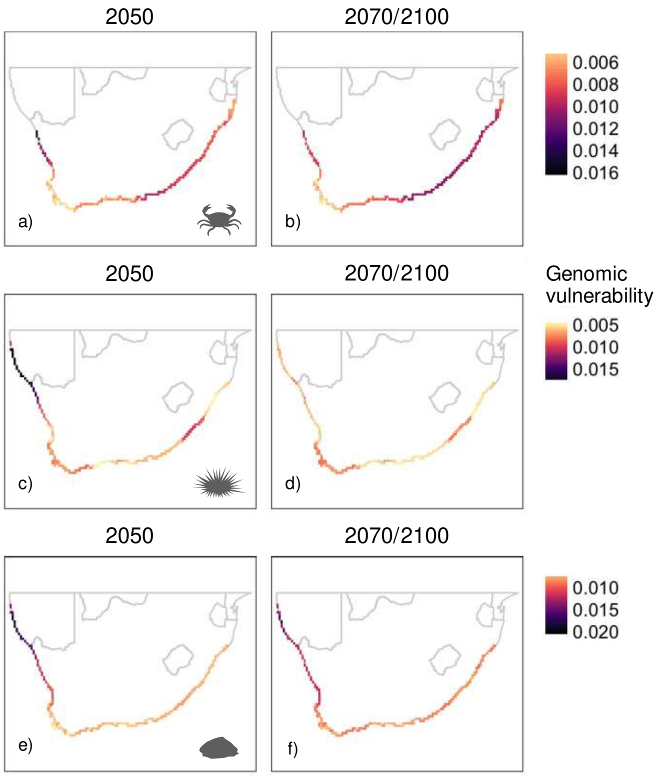

Figure S7. Genomic vulnerability patterns of neutral SNPs, calculated as Euclidean distance between current and future genetic spaces, shown for RCP 4.5 scenario for 2050 (a, c, e), and 2070/2100 (b, d, f; 2070 for landscape features, 2100 for seascape features), for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Darker shaded regions represent areas of higher genomic vulnerability, where genomic composition will be altered the most to track environmental changes.

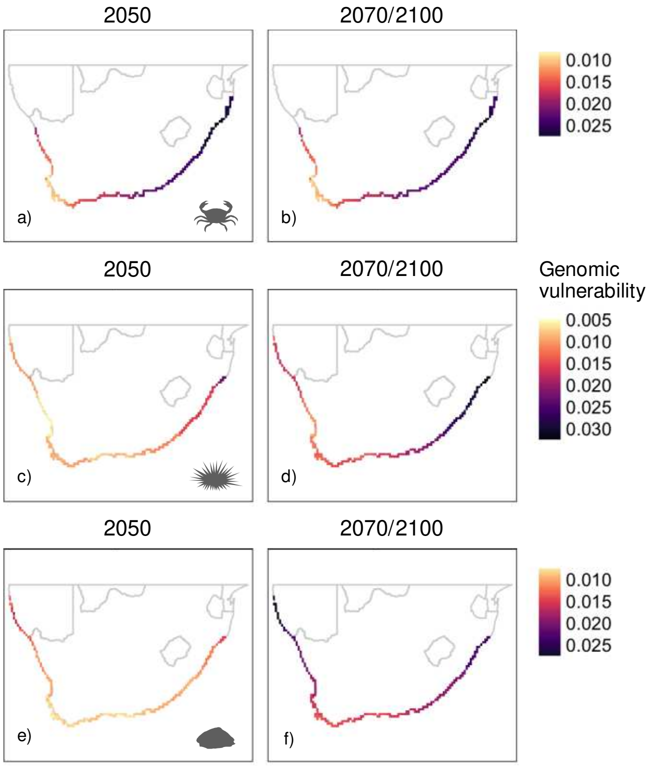

Figure S8. Genomic vulnerability patterns of neutral SNPs, calculated as Euclidean distance between current and future genetic spaces, shown for RCP 8.5 scenario for 2050 (a, c, e), and 2070/2100 (b, d, f; 2070 for landscape features, 2100 for seascape features), for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Darker shaded regions represent areas of higher genomic vulnerability, where genomic composition will be altered the most to track environmental changes.

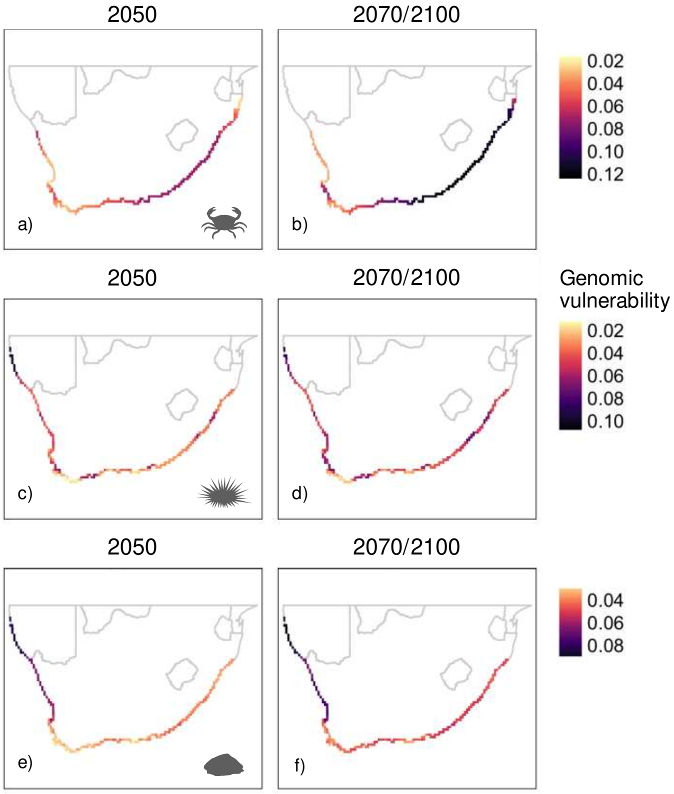

Figure S9. Genomic vulnerability patterns of outlier SNPs, from models including the same four environmental predictor variables as in the species distribution models (minimum and maximum air temperature, and mean sea-surface salinity and temperature), shown for RCP 4.5 for 2050 (a, c, e), and 2070/2100 (b, d, f; 2070 for landscape features, 2100 for seascape features), for *C. punctatus* (a, b), *P. angulosus* (c, d), and *S. granularis* (e, f). Darker shaded regions represent areas of higher genomic vulnerability, where genomic composition will be altered the most to track environmental changes.