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Title: Multi-species genetic objectives in spatial conservation planning

Running title: Multi-species genetic conservation planning

Abstract

The growing threats to biodiversity and global alteration of habitats and species distributions make it increasingly necessary to consider evolutionary patterns in conservation decision-making. Yet there is no clear-cut guidance on how genetic features can be incorporated into conservation planning processes, with multiple molecular markers and several genetic metrics for each marker type to choose from. Genetic patterns also differ between species, but the potential trade-offs amongst genetic objectives for multiple species in conservation planning are currently understudied. This study compares spatial conservation prioritizations derived from two metrics of both genetic diversity (nucleotide and haplotype diversity) and genetic isolation (private haplotypes and local genetic differentiation) for mitochondrial DNA for five marine species. The findings show that conservation plans based solely on habitat representation noticeably differ from those additionally including genetic data, with habitat-based conservation plans selecting fewer conservation priority areas. Furthermore, all four genetic metrics selected approximately similar conservation priority areas, which is likely a result of prioritizing genetic patterns across a genetically diverse array of species. Largely, the results suggest that multi-species genetic conservation objectives are vital to create protected area networks that appropriately preserve community-level evolutionary patterns.

Keywords: genetic diversity, genetic isolation, Marxan, conservation genetics, spatial prioritization, inter-tidal ecology

Introduction

Anthropogenic pressures such as overfishing, movement of alien species, habitat alteration and human mediated climate impacts are major drivers of change in marine ecosystems (Halpern et al. 2008; Mead et al. 2013). In order to combat further degradation of marine and coastal environments and to provide resilience for the future, marine protected areas (MPAs) have been shown to be an effective management tool (Edgar et al. 2014). However, limited resources and high socio-economic dependencies of local communities on marine ecosystem services requires a balance of marine conservation objectives and the associated costs of conservation actions (Bottrill et al. 2008). To accommodate trade-offs in conservation planning, quantitative approaches are often implemented and are highly effective at identifying locations best suited for conservation action (Wilson et al. 2009).

Evidence-based conservation prioritization processes usually involve setting objectives to conserve specific amounts of spatially explicit biodiversity features such as habitat type, species richness, or migration patterns (Margules & Pressey 2000; Leslie 2005), and then reaching these objectives in the most cost-efficient manner (Naidoo et al. 2006). However, while biodiversity features such as habitat type or species distributions are important to include in conservation plans, and have informed the vast majority of spatial plans to date, they fail to represent evolutionary patterns such as phylogenetic diversity (Mouillot et al. 2016), population structure (von der Heyden 2009) and local adaptation (McMahon et al. 2014). Because standing genetic variation can play a major role in providing resilience to future change (Ehlers et al. 2008), it is essential that conservation objectives incorporate genetic patterns both within and between species (Pressey et al. 2007; Sgrò et al. 2010). Some efforts have been made to integrate genetic metrics from single species (Sork et al. 2009; Beger et al. 2014), and surrogates for genetic patterns across multiple species (Carvalho et al. 2010) into conservation planning, yet the integration of multiple genetic metrics from multi-species data sets is currently lacking within conservation planning theory.

Much empirical work has been done on spatially delineating populations and conservation units using genetic information (Moritz 2002; Funk et al. 2014). However, the actual implementation of

genetic data into conservation planning remains an exception and not the rule (von der Heyden 2009; Laikre 2010), particularly in marine systems (Beger et al. 2014; von der Heyden et al. 2014). Ambiguity in the interpretation of genetic data and a need for a framework to guide its use hinder the integration of genetic metrics into spatial planning (Waples et al. 2008; Shafer et al. 2014). For example, objectives need to be clear and measurable, define relevant spatial and temporal scales, and address environmental and socio-economic uncertainty (Mace & Purvis 2008; Kool et al. 2015). Nonetheless, there are examples of genetic metrics within conservation objectives, such as delineating stocks for fisheries management or assessing gene flow (von der Heyden et al. 2014) and advancements have been made on formulating objectives for genetic metrics in conservation planning (see Beger et al. 2014). The next step towards operational conservation planning for evolutionary processes requires integrating planning objectives for various genetic metrics across multiple species as conservation features.

Therefore, this study compares conservation scenarios based on objectives from four genetic metrics, namely haplotype diversity (h), nucleotide diversity (π) (*sensu* Nei 1987), number of private haplotypes, and local genetic differentiation (Table 1), from five rocky shore species. These genetic metrics are highly relevant to conservation as they capture historical and contemporary processes shaping extant patterns of biodiversity.

For example, genetic diversity is recognized as being an important conservation feature as high levels of genetic diversity and variation in genotypes/haplotypes can increase individual fitness and population resilience (Hughes et al. 2008) and is the raw material for natural selection to act on (Lande & Shannon 1996). Further, there is evidence that genetic diversity may correlate with species richness (Messmer et al. 2012; Wright et al. 2015; Selkoe et al. 2016), and potentially enhance ecosystem function and resilience (Reusch et al. 2005; Bernhardt & Leslie 2012). Conversely, low genetic diversity makes a population more susceptible to inbreeding depression and possible extinction (Charlesworth & Charlesworth 1987).

Additionally, meta-population persistence and individual population resilience can be inferred by comparing the genetic distinctiveness of populations (Mortiz 2002; Beger et al. 2014). If a population is genetically isolated, it may be less resilient (Van Oppen & Gates 2006; Vollmer &

Palumbi 2007) and should be delineated as an individual management unit (Palumbi 2003). Therefore, such populations have conservation importance simply because they are different, making them analogous to a rare species. Further, unique genotypes/haplotypes or rare haplotype frequencies may be a result of natural selection, which in the absence of markers that measure adaptive variation could indicate local adaptation if ecological or environmental factors are driving genetic patterns. On the contrary, low distinctiveness and uniqueness is also of conservation value because populations that are not in isolation are genetically and demographically connected, making them potentially more resistant and resilient to change.

In order to streamline the inclusion of genetic information into conservation planning processes, it is crucial to first understand how different metrics of genetic diversity and differentiation compare within a conservation planning framework. Hence, this paper aims to compare conservation scenarios from four genetic metrics for five phylogenetically and functionally different species. Broadly this study asks the following questions: 1) do priorities differ for genetic-based conservation plans, compared to a baseline using only habitat-based objectives?; 2) do priorities differ between conservation plans based on different genetic diversity and isolation metrics?; 3) what is the effect of averaging genetic metrics from multiple species rather than incorporating them individually?; and finally 4) do multiple species and genetic metrics contribute equally to the combined conservation outcome? Answers to these questions are a prerequisite to formulating a generalizable framework for conserving multi-species genetic patterns.

Methods

This study focuses on the west coast of South Africa (bounded by 18.3'E, -34.1'S and 16.8'E, -29.3'S). We included genetic data from five obligate rocky shore species that share similar distributions along the South African coastline. All species were collected from the same seven sites along the South African west coast (Fig. 1), one of South Africa's most threatened marine environments (Sink et al. 2011).

106 The five species for which we included genetic data are the granular limpet (*Scutellastra*
107 *granularis*), super klipfish (*Clinus superciliosus*), Cape urchin (*Parechinus angulosus*), tiger topshell
108 winkel (*Oxystele tigrina*) and cushion star (*Parvulastra exigua*). These species were chosen due to their
109 different life history characteristics, reproductive strategies and functional roles within the rocky shore
110 community (Table 1 Supporting Information; Mertens 2012). Several studies suggest that these five
111 species exhibit complex evolutionary histories along the west coast of South Africa (von der Heyden et
112 al. 2011; Muller et al. 2012; Wright et al. 2015). Based on mitochondrial DNA (mtDNA) datasets, the
113 five study species display variable genetic structure, different migration rates and a wide range of
114 genetic diversity values (Tables 1 & 2 Supporting Information; Mertens 2012). Therefore, we expect
115 them to represent the genetic spectrum of species within the regional rocky shore community.
116
117 *Genetic metrics*
118 The four genetic metrics (haplotype diversity (h), nucleotide diversity (π), number of private
119 haplotypes, and local genetic differentiation) were derived from mtDNA regions, specifically a
120 fragment of the cytochrome oxidase I (COI) gene for the invertebrates and a section of the mtDNA
121 control region for the klipfish (*C. superciliosus* – Table 1 Supporting Information). The evolutionary
122 mechanisms of mtDNA are well understood from a comparative phylogeographic and evolutionary
123 perspective (Bowen et al. 2014), making mtDNA regions useful markers for integrative genetic
124 conservation planning efforts.
125
126 *Data generation and implementation*

127 We used TCS (Clement 2000) to collapse all genetic datasets into haplotypes and Arlequin v3.5
128 (Excoffier et al. 2010) to calculate π and h. Local genetic differentiation was calculated in Arlequin,
129 with a sequential AMOVA including two populations; one being the site of interest, and the other being
130 all sites combined. Unique haplotypes were counted and labeled as private haplotypes for each
131 population. We then interpolated the genetic data from the seven point localities using an inverse
132 distance weighting technique in ArcGIS v10.2 (ESRI 2014). We recognize that this procedure

133 represents a simplified version of natural genetic patterns, and that genetic point data should rather be
134 predicted using environmental parameters, yet there is currently no framework on how to model genetic
135 patterns in marine environments (Beger et al. 2014).

136 For each genetic metric, we created three classes (low, medium, high) using equal intervals
137 across their measured range of values and set conservation targets for each class. However, to set
138 appropriate targets for each genetic metric, it is important to first identify conservation objectives
139 (Carwardine et al. 2009). Here, our conservation objective was to represent regional genetic variability
140 to include evolutionary significant areas into a marine reserve network. We followed a similar protocol
141 to Beger et al. (2014) and set the target to represent 50% of the high and low classes, and 30% of the
142 medium class, as the low and high classes are vital for both single and meta-population persistence,
143 whereas the middle class is a precautionary target for areas that may turn into low or high ranking sites
144 in the future.

145 Spatial prioritizations incorporating genetic metrics were carried out for each of the five species
146 individually, as well as a sixth scenario including values averaged across all five species for each of the
147 seven sampling locations. Averaging the values for each genetic metric summarizes the interspecific
148 genetic composition within the planning region, and may identify important areas for conserving
149 ecosystem function (Whitham et al. 2006; Hersch-Green et al. 2011). This 'community genetics'
150 approach may be more effective with large data sets (such as in Wares et al. 2002; Selkoe et al. 2016),
151 but its applicability to spatial management has yet to be explored.

152

153 *Conservation prioritization analyses*

154 Conservation priority areas were identified with Marxan, a decision support tool that uses an
155 algorithm to minimize the reserve system cost of the entire network, whilst meeting a set of biodiversity
156 targets (Ball et al. 2009). Our planning domain included near-shore intertidal areas along the ~800km
157 length of the west coast of South Africa (Fig 1A), extending 500m seaward to 500m inland. The
158 baseline conservation features are five rocky shore habitat types identified in the 2011 National
159 Biodiversity Assessment (Sink et al. 2011); namely exposed, sheltered, mixed, boulder and hard ground

160 rocky shores. After performing a sensitivity analysis, we chose a conservation target to include 40% of
161 each habitat. To represent lost exploitation opportunities, we included cost data from Majiedt et al.
162 (2013), which quantifies a diverse array of socio-economic pressures currently identified along the
163 South African west coast. The habitat and cost features remained constant across all planning scenarios
164 and are termed 'baseline' for the remainder of this study.

165 In order to explore the effect of each genetic metric, as well as each of the five species on
166 conservation priorities, we compared trade-offs between variables using the following: 1) A genetic
167 metric approach where each metric was included separately for all species (change in genetic metric); 2)
168 A species approach where all genetic metrics were included for each species separately (change in
169 species); 3) A combined approach where each genetic metric was included separately for each species
170 (termed ALL); and 4) An averaged approach where genetic metrics were averaged across the five
171 species resulting in one spatial dataset per genetic metric (termed AVG; Table 2). The conservation
172 targets of 50% and 30% remained the same for each genetic feature across the scenarios.

173 Additionally, to examine the effects of different conservation objectives, we chose a single
174 metric, local genetic differentiation, and solely protected either high or low ranking areas. For the
175 objective of conserving genetically distinct areas, we set the target to protect 60% of high-ranking areas,
176 and zero percent of the medium and low ranking areas. For the counter objective of conserving
177 genetically connected sites we set the target to conserve 60% of low ranking areas and zero percent of
178 the medium and high ranking areas.

179 For each of the scenarios, we ran Marxan 100 times to account for variability across solutions,
180 and maintained calibration parameters constant. We then followed the protocols in Harris et al. (2014)
181 to analyze similarities between scenarios, performing non-metric multi-dimensional scaling (nMDS)
182 ordination based on Jaccard resemblance matrices in R 3.2.2 (R Development Core Team 2012).

183 Finally, to quantify spatial similarities between scenarios we calculated Pearson correlation
184 coefficients (from selection frequency values for each planning unit) between each pair of scenarios. To
185 obtain the average amount of congruence between scenarios with either a change in species or genetic
186 metric, we then took the average of the Pearson correlation coefficients for each of the two scenario

groupings. To further quantify the trade-offs associated with either a change in species or genetic metric, we calculated the range in number of selected planning units, as well as Marxan cost and score from both scenarios with a change in species or genetic metric.

Results

Spatial conservation priorities

High-priority sites for conservation differ between the baseline scenario and each genetic scenario (Fig. 1, B-H), yet all scenarios highlight areas along the entire coastline as priority sites. There are minor differences between the genetic scenarios, with each one identifying multiple clusters of conservation priority areas, roughly extending from those chosen in the baseline scenario (Fig. 1, E-H). The haplotype diversity scenario has the most definitive high priority clusters (Fig. 1, E), followed by the local genetic differentiation scenario (Fig.1, G). Both the private haplotypes and nucleotide diversity scenarios show smaller conservation priority clusters that are more spread out along the coastline (Fig. 1, F,H). Lastly, the planning units chosen throughout all genetic scenarios (Scenarios 2-5) indicate that the northern region, as well as select areas throughout the mid-and southern west coast are conservation genetic 'hotspots' (Fig. 2).

Scenario dissimilarities

The baseline scenario forms a distinct cluster and is highly dissimilar from the genetic scenarios (Fig. 2A). Solutions from each genetic scenario form a distinct cluster, with little overlap between scenarios (Fig. 2B). The scenarios including nucleotide diversity and number of private haplotypes for all species are the most similar, followed by those including haplotype diversity and local genetic differentiation. The ALL scenario shows a broad range of solutions, of relatively equal similarity to each of the scenarios including one genetic metric. Lastly, the scenario with averaged genetic metrics is most dissimilar to all of the other genetic scenarios and there is no congruence between the two scenarios that include all genetic metrics (ALL and AVG).

The nMDS plot based on the dissimilarities between single species and multi-species genetic scenarios (Fig. 2C) shows little concordance between the solutions, with each species highlighting different conservation priority areas. Most single-species scenarios form tight clusters with highly similar solutions, with the exception of the granular limpet (*S. granularis*), which shows a broad range of spatial solutions. The two scenarios including all species (ALL and AVG) show no congruence, with the AVG scenario displaying the most divergent set of solutions.

Quantified conservation trade-offs

The Pearson correlation coefficients mirror the nMDS plots (Table 3, Supporting Information) and show that no one solution is highly dissimilar to the others with the exception of the baseline scenario. The average similarity between scenarios with a change in genetic metric is just slightly lower than the scenarios with a change in species (Table 2). However, the ranges in number of selected planning units, Marxan cost and score are larger across the scenarios with a change in species versus a change in genetic metric (Table 2).

Discussion

Intraspecific genetic variation is the foundation of biological diversity, and thus conserving the adaptive potential of organisms is pivotal to their long-term persistence. Despite calls to inform conservation decisions with genetic and genomic information (Funk et al. 2014; Shafer et al. 2014), few examples exist where evolutionary patterns have been translated into actionable conservation objectives (Laikre 2010) with existing studies focusing solely on single species (Sork et al. 2009; Beger et al. 2014; von der Heyden et al. 2014). Importantly, our findings demonstrate that no single species can adequately represent multi-species genetic patterns because spatial conservation priority sites vary between different species. Further, within the context of understanding habitat-only versus genetic scenarios, each scenario including a genetic metric highlights noticeably more priority areas compared to the baseline scenario. This indicates that not accounting for community genetic metrics in

241 conservation plans will underrepresent genetic patterns in MPA networks, thereby jeopardizing the
242 protection of the processes driving spatial patterns of biodiversity (Klein et al. 2009).
243
244 *Conservation planning with and without genetic data*
245 We found a clear separation between conservation priority areas derived from the baseline
246 scenario and the genetic scenarios, confirming similar results for data from a single species (Beger et al.
247 2014). While conservation priority areas from each genetic metric seem to roughly correlate to those in
248 the baseline scenario, the priority sites chosen throughout all genetic scenarios (Fig. 2, D) are not
249 representative of the baseline, meaning that genetic 'hotspots' are not spatially associated with the
250 different habitat types. Using multi-species conservation objectives, we show that dissimilarities
251 between habitat-based and genetics-based conservation plans result in widely different scenarios,
252 further supporting the need to include genetic information into conservation planning (von der Heyden
253 2009). In the context of a rapidly changing climate, this finding has important implications for the
254 persistence of species and communities, as failing to protect standing genetic variation increases the
255 likelihood of losing genetic variants which may be more resilient to change (Barrett & Schulter 2008).
256
257 *Conservation trade-offs between genetic measures*
258 All genetic scenarios choose approximately similar areas as conservation priorities, with slight
259 discrepancies in conservation selection patterns (Fig. 1, E-H). This suggests that protecting a percentage
260 of high, medium and low ranking areas for a single genetic metric from multiple species will most
261 likely also capture priority sites arising from other genetic metrics. The broadly similar conservation
262 priorities between the different genetic metrics are unexpected, as different evolutionary and
263 demographic processes and statistical approaches relate to the different metrics (Table 1). The
264 similarities between the conservation priority areas from the separate genetic metrics could be a result
265 of the broad spectrum of genetic patterns within our five study species. For instance, when different
266 conservation objectives (conserving only high or low ranking areas) are compared from just a single
267 metric (local genetic differentiation), we find that some sites are chosen as conservation priority areas

for both objectives (Fig. 3). This illustrates that while the genetic metrics may have different spatial patterns, these differences can be captured in the conservation solutions in some instances without spatial rearrangement of priorities.

Whilst the different genetic metrics broadly select similar conservation priority areas along the coastline, there are discrepancies between the different genetic scenarios. For instance, the scenarios including nucleotide diversity and private haplotypes leads to smaller, but more widely spread areas of conservation priority when compared to those based on haplotype diversity and local genetic differentiation (Fig. 1, E-H). The similar conservation priorities between nucleotide diversity and private haplotypes, and haplotype diversity and local genetic differentiation are unexpected, as it would be likely that the two scenarios including either a diversity (h / π) or isolation (private haplotypes / local genetic differentiation) metric would be more similar to each other. However, the similar conservation spatial patterns between nucleotide diversity and private haplotypes in our study are most likely because there is little agreement in the genetic values between species, which leads to the more widely spread selection of planning units.

Conservation trade-offs across different species

Each of the five study species shows highly variable conservation solutions (which is expected since each species is characterized by unique genetic characteristics), with little congruence between scenarios representing different species (Fig. 2B). Larval dispersal is recognized as an important driver of these differences (White et al. 2010), but the interaction between pelagic larval duration and population structure varies hugely between species (Selkoe & Toonen 2011). Furthermore, interspecific genetic differences can be due to forces unrelated to dispersal, such as habitat availability and time since re-colonization (Selkoe et al. 2014; Selkoe et al. 2016). Therefore, the inclusion of genetic information from multiple species, even if they have similar biological characteristics (e.g. distribution ranges, life history) is critical, as even functionally similar species can be characterized by very different evolutionary histories and contemporary genetic patterns (Wright et al. 2015). Moreover, the results show little congruence between phylogeographic patterns and conservation spatial patterns, as

295 the two most highly structured species (*P. angulosus* and *P. exigua*) and the two panmitic species (*S.*
296 *granularis* and *O. tigrina*) do not have spatial solutions that are more similar to each other than those
297 species with different phylogeogpraphic patterns (Fig. 2C; Table 2 Supporting Information). In
298 addition, the number of selected planning units also does not correspond with phylogeographic patterns,
299 as the scenarios with the highest number of selected planning units are from *P. angulosus* and *S.*
300 *granularis*, which have the highest and lowest genetic structure respectively (Table 2; Table 2
301 Supporting Information). This suggests that if the objective is to identify genetically diverse or unique
302 areas, then solely including phylogeographic patterns may not capture the full extent of genetic
303 relationships between sites.

304 Our findings also show distinct conservation priorities occur with the inclusion of either single-
305 species or multi-species genetic metrics (Fig. 2B). While the inclusion of multi-species objectives is
306 recommended in conservation planning (von der Heyden 2009; Toonen et al 2011; Magris et al. 2015),
307 no previous studies have explored how conservation objectives aimed at protecting community-level
308 genetic composition compare with those aimed at single species as indicators for overall genetic
309 variability. We show that including genetic information for multiple species independently (ALL
310 scenario) gives conservation priorities that are equally similar to the priorities derived from genetic data
311 from each individual species (Fig. 2, C; Table 3 Supporting Information). Thus, we recommend
312 including multiple species as features individually instead of using the multi-species average as a single
313 conservation feature in conservation planning (Fig. 2, A-C). However, averaging genetic metrics may
314 be a viable approach with larger or more homogeneous data sets. For example, Selkoe et al. (2016)
315 found that within a 47 species genetic dataset, many species showed compatible genetic patterns, which
316 lends some support for averaging genetic measures. Further, the effects of averaging genetic datasets
317 with missing data has yet to be explored, as well as the potential trade-offs of having multiple species
318 with averaged values versus having fewer species with non-averaged values.

319

320 *Conservation trade-offs across genetic metrics and species*

We found that the average similarity between spatial priorities is only slightly larger with a change in species versus change in genetic metric. This implies that the inclusion of either an additional genetic metric or species will alter the conservation priorities to a similar degree. However, the results also show that the scenarios with a change in species lead to a greater range in number of planning units chosen, as well as Marxan cost and score, which means a change in species is more likely to result in conservation solutions with a broader range in priority areas chosen in the 'optimum' spatial plan. The results suggest that a change in species leads to an overall greater change in number of planning units selected (which in turn leads to greater trade-offs in cost and score), yet the areas where the planning units are selected will spatially be more similar to each other with a change in species than genetic metric.

Concluding remarks

This study shows that, using mtDNA as a marker, conservation plans can be developed to preserve not only habitat features, but also the evolutionary aspects of species distributions. Given that a majority of studies dealing with population genetic structure to date have used mtDNA as one of the markers (Bowen et al. 2014; Keyse et al. 2014), there is ample opportunity for exploring the approaches laid out here with different species and geographical areas. For example, there are a large number of single and multi-species genetic data sets available for the Indo-Pacific (see Horne et al. 2008; Gaither et al. 2010; Keyse et al. 2014) and the Mediterranean (see Carlsson et al. 2004; Duran et al. 2004; Carreras et al. 2007), which could be utilized and included into management plans. Although the results from this study suggest that a change in genetic metric does not lead to substantial trade-offs in conservation priorities, this is less likely to be the case with metrics from several molecular markers, because different markers should, in theory, capture evolutionary patterns specific to the region of the genome they characterize. Several additional aspects, such as comparing conservation priority areas derived from both neutral and adaptive markers, and including both local and pairwise genetic measures remain to be explored, however our work provides a baseline for investigating these conservation scenarios. In addition, with the development of landscape genetics and genotype-by-environment tests,

it should become possible to derive environmental or ecological factors driving genetic patterns in natural systems. This information may help predict future changes in genetic variation and allow us to account for such changes within conservation planning frameworks.

Supporting Information

Life history traits (Appendix S1) and genetic variation indices (Appendix S2) for the five study species are available online, along with quantitative trade-offs between scenarios (Appendix S3). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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570
571 Table 1- The four genetic features compared in this study, what they measure, and their relevance to
572 conservation planning.
573

Genetic feature	Definition	Conservation relevance
Haplotype diversity (*h*)	- The probability that two randomly sampled individuals differ in their haplotypes (a.k.a. mitochondrial DNA allele types)	- As haplotype diversity represents frequency-weighted variation (Nei 1987), it incorporates gene flow, which may make it a more suitable metric to identify management units (Funk et al. 2014)
Nucleotide diversity (π)	- The average number of nucleotide differences per site between any two DNA sequences chosen randomly from the sample population	- Nucleotide diversity represents the absolute standing genetic variation, which may make it a more suitable metric to identify evolutionary significant units (Funk et al. 2014)
Number of private haplotypes	- Private haplotypes (or alleles) are unique to a single population -A measure of how unique a site is compared to other sites	- A site with a high number of private haplotypes might be genetically isolated, rendering it less resilient to stochastic, catastrophic features such as oil spills (Lande & Shannon 1996) - Genetically unique

		populations may be interpreted as evolutionary hotspots (Beger et al. 2014)
Local genetic differentiation	- A measure of how much a population's genetic diversity differs from the mean of all of the populations combined	- If a population is genetically isolated from the other populations then it may be less resilient - A population may also be genetically distinct due to local evolutionary processes, in this case the site can play an important role in the meta-population (Beger et al. 2014)

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575
576 Table 2- Describes the various scenarios compared in Marxan.
577

Scenario No.	Conservation features included	Abbreviation
1	Habitat type (baseline)	B
2	Haplotype diversity	H
3	Nucleotide diversity	N
4	Local genetic differentiation	L
5	Private alleles	P
6	All genetic metrics for *C. superciliosus*	CS
7	All genetic metrics for *O. tigrina*	OT
8	All genetic metrics for *P. angulosus*	PA
9	All genetic metrics for *P. exigua*	PE

10	All genetic metrics for *S. granularis*	SG
11	All genetic metrics as five individual layers corresponding to each species	ALL
12	Each genetic metric as single layer averaged over the five species	AVG

Table 3- Measures of dissimilarity across scenarios altering either the species or genetic feature included as conservation features.

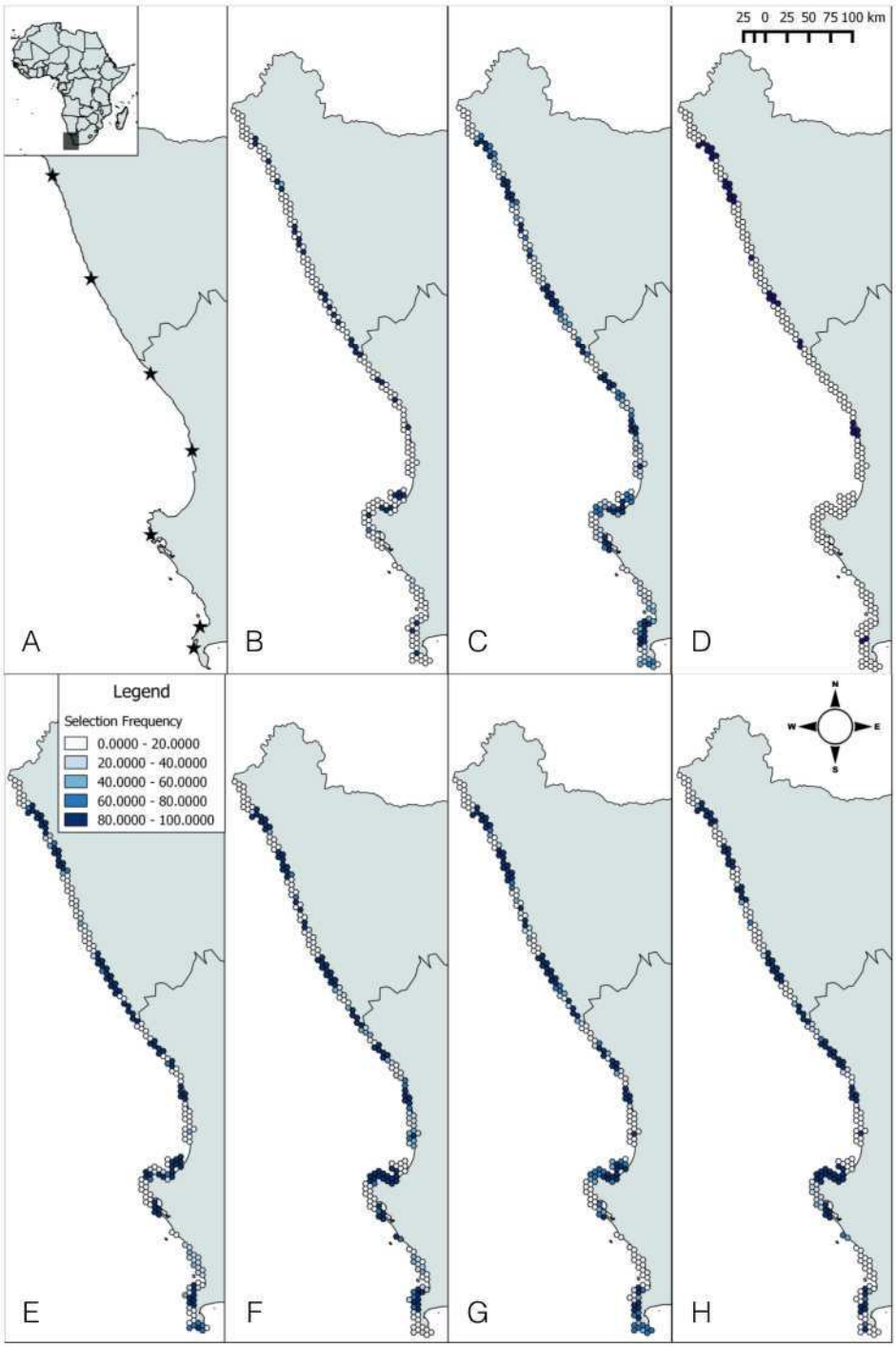
Measure of dissimilarity	Change in species	Change in genetic feature
Average Pearson correlation	0.61	0.56
Range in cost	95	50
Range in score	91	44
Range in planning units	7	5

Figure Legends

Fig. 1- The seven sampling locations (A) and conservation priorities from the Baseline (B), ALL (C), Haplotype diversity (E), Nucleotide diversity (F), Local genetic differentiation (G), and Private haplotype (H) scenarios, as well as planning units chosen by each genetic metric scenario (D). Conservation priority maps are based on selection frequencies; darker planning units have a higher selection frequency.

Fig. 2- Non-metric multi-dimensional scaling ordination plots illustrating the dissimilarities between the 100 solutions of the baseline and genetic scenarios (A), solely the genetic scenarios (B), as well as the single-species scenarios (C).

Fig. 3- The conservation spatial patterns derived from conserving 60% of either low genetic differentiation (A) or high differentiation (B). Areas highlighted in red are selected with both objectives.



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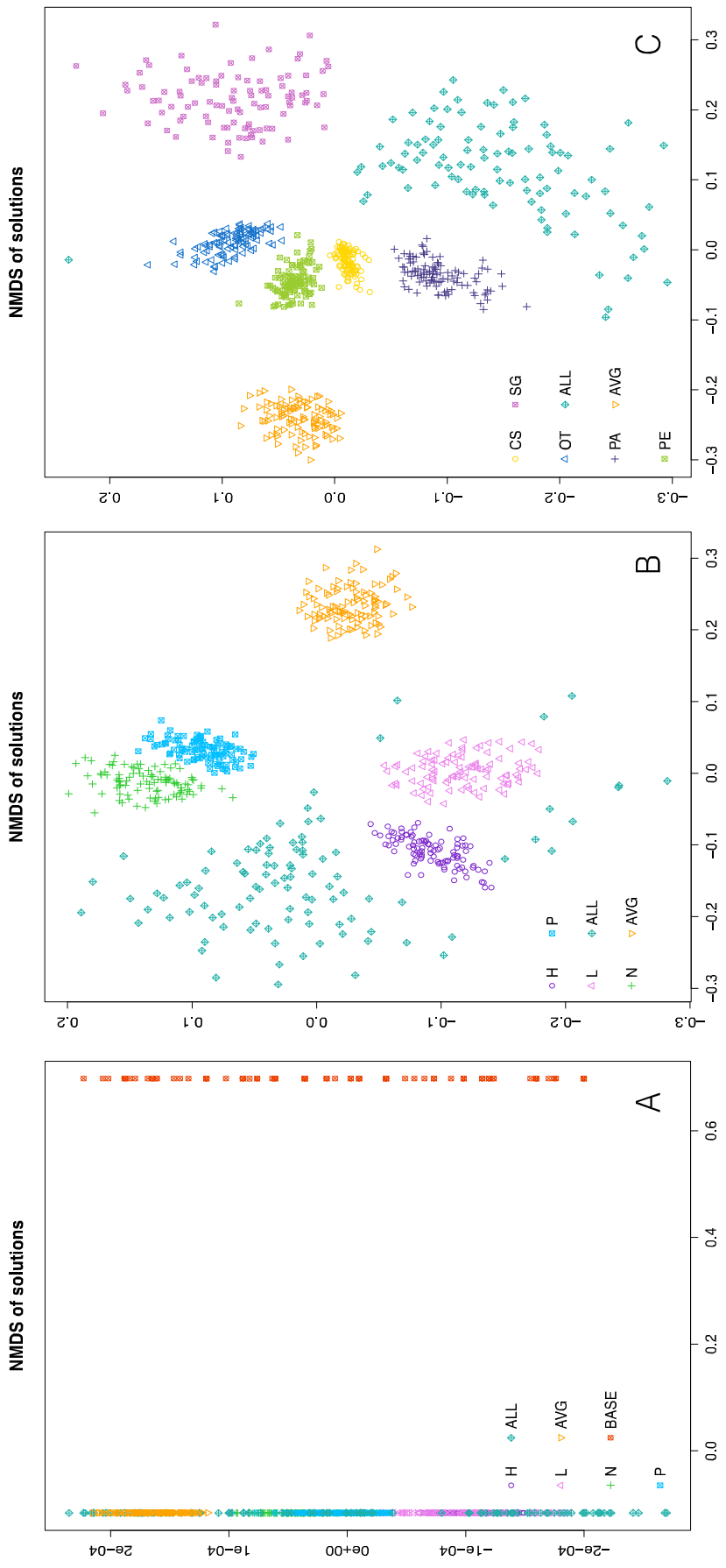
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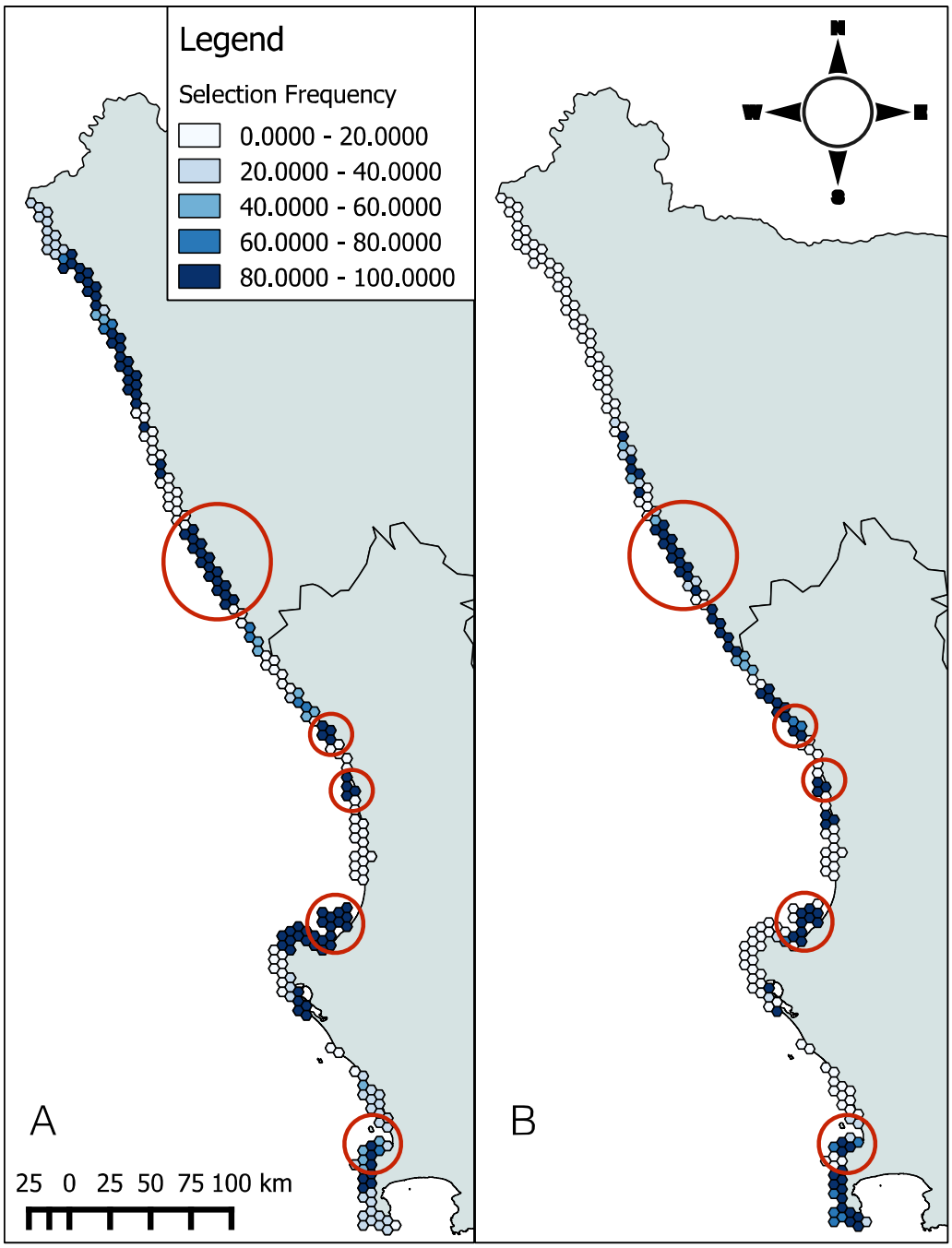
Legend
Selection Frequency
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40.0000 - 60.0000
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80.0000 - 100.0000
A
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Supporting Information

Supporting Information 1- Life history characteristics of the five study species

Table 1- Summary of life history characteristics

Our five study species represent a phylogenetically diverse assemblage of rocky shore species and are generally abundant on South African rocky shores. The table below summarizes some of their life history characteristics (after Table 1 in Wright et al. 2015). Additional information was taken from Payne et al. (2015).

Species	Common name	Phylum	Fertilization type	Min pelagic larval duration (days)	Diet	Position on rocky shore
Clinus superciliosus	Super klipfish	Chordata	Internal, live young	0	Carnivore	Subtidal- high
Oxystele tigrina	Tiger topshell	Mollusca	Spawns	4-6 (sister species)	Grazer	Mid shore
Scutellastra granularis	Granular limpet	Mollusca	Spawns	4-10 (sister species)	Grazer	High shore
Parechinus angulosus	Cape urchin	Echinodermata	Spawns	49-56	Grazer	Mid to low shore
Parvulastra exigua	Cushion star	Echinodermata	Brooder, crawl-away young	0	Grazer	Mid to low shore

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Supporting Information 2- Genetic data acquisition and genetic values included into Marxan analyses

Genetic data generation

Data sets were generated by and taken from Mertens (2012; *S. granularis*, *O. tigrina*, *P. exigua*, *C. superciliosus*), with the exception of *P. angulosus* which correspond to sequences from Muller et al. (2012) and some sequences of *C. superciliosus* (von der Heyden et al. 2011). Briefly, DNA was extracted using the Nucleo-Spin DNA extraction kit (Machery-Nagel), followed by PCR amplification following the protocols of Folmer et al. (1994) and Palumbi et al. (1991) for mtDNA COI, and Lee et al. (1995) for the mtDNA control region. After visualizing on a 1% agarose gel stained with ethidium bromide, PCR products were sent for sequencing on an ABI-3100 automated sequencer (Applied Biosystems) at the Central Analytical Facility at the University of Stellenbosch. Alignments were created in BioEdit v7.0.9.0 (Hall 1999) and all new sequences were deposited in GenBank under the following Accession Numbers: KU64040 - KU640590, KU640591 - KU640755 and KU640756 - KU640952.

693 **Table 2-** The genetic metrics that were normalized, interpolated and included into Marxan as

694 conservation features.

Location	Kommetjie	Sea Point	Jaccobsbaai	Lambertsbaai	Brandsebaai	Hondeklipbaai	Port Nolloth
Haplotype Diversity (*h*)							
C. superciliosus	0.90	0.94	0.93	0.92	N/A	0.91	0.96
P. exigua	0.80	0.61	0.46	0.56	0.80	0.68	0.34
P. angulosus	0.95	0.92	0.97	0.97	0.83	0.84	0.93
S. granularis	0.88	0.83	0.90	0.95	0.96	0.89	0.94
O. tigrina	0.88	0.91	0.92	0.90	0.87	0.89	0.91
Nucleotide Diversity (π)							
C. superciliosus	0.0080	0.0089	0.0059	0.0128	N/A	0.0121	0.0123
P. exigua	0.0001	0.0015	0.0008	0.0015	0.0028	0.0019	0.0009
P. angulosus	0.0114	0.0134	0.0114	0.0163	0.0027	0.0033	0.0031
S. granularis	0.0040	0.0036	0.0037	0.0053	0.0044	0.0043	0.0050
O. tigrina	0.0051	0.0052	0.0061	0.0046	0.0055	0.0049	0.0052
Private Haplotypes (#)							
C. superciliosus	8	8	9	1	N/A	8	13
P. exigua	1	3	3	0	1	4	2
P. angulosus	11	8	13	12	5	8	11
S. granularis	5	6	4	10	9	8	8
O. tigrina	8	4	6	5	2	1	3

	Local genetic differentiation						
C. superciliosus	0.0663	0.1094	0.0617	0.0650	N/A	0.1343	0.0333
P. exigua	0.0885	0.0553	0.0414	0.2205	0.0833	0.3755	0.0231
P. angulosus	0.3519	0.2392	0.0116	0.0231	0.1625	0.0166	0.1712
S. granularis	0.0008	0.0023	0.0201	0.0137	0.0074	0.0128	0.0009
O. tigrina	0.0103	0.0087	0.0019	0.0133	0.0137	0.0013	0.0028

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Supplementary Materials 3- Quantitative trade-offs between scenarios with a change in species versus change in genetic metric.

Table 1- Pearson correlation coefficients corresponding to each pair of scenarios with a change genetic metric.

	B	H	N	L	P	ALL
B						
H	0.37					
N	0.27	0.62				
L	0.33	0.72	0.61			
P	0.26	0.59	0.74	0.63		
ALL	0.38	0.81	0.80	0.78	0.70	
AVG	0.37	0.50	0.56	0.57	0.52	0.61

Table 2 - Pearson correlation coefficients corresponding to each pair of scenarios with a change in species.

	B	**CS**	**OT**	**PA**	**PE**	**SG**	**ALL**
B							
CS	0.35						
OT	0.39	0.74					
PA	0.41	0.83	0.72				
PE	0.41	0.83	0.71	0.70			
SG	0.29	0.67	0.68	0.63	0.69		
ALL	0.38	0.78	0.81	0.83	0.76	0.81	
AVG	0.37	0.60	0.61	0.62	0.64	0.47	0.61