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Highlights

- Different molecular metrics should be used to meet specific conservation objectives
- Single-species molecular data are inefficient at capturing multi-species evolutionary potential
- Genetic data may be a potential surrogate of genomic data within conservation planning

Abstract

Emerging global change stressors have underlined the importance of informing conservation decisions with molecular diversity, particularly including intraspecific adaptive or evolutionary potential across species and populations. Population-level evolutionary potential is best captured by genomic approaches, yet these data types mostly remain limited to model organisms. In contrast, traditional genetic data are broadly available. The relevance of genomic metrics, and how they differ from genetic metrics in the context of spatial conservation practices, remains unknown. This provides an opportunity to consider the relative contribution and impact of genomic compared to genetic metrics in their efficiency of selecting conservation areas of evolutionary importance. Here, we provide a guideline to include metrics of genetic and genomic variation into spatial planning analyses for multiple conservation objectives, and empirically explore how spatial prioritizations change when including different types of molecular information across multiple species. Specifically, we compare conservation solutions of scenarios including either an increase in molecular information (i.e. either a single locus; mtDNA, or several thousand loci; SNPs), or an increase in species included. We find that including less molecular information from many species leads to similar outcomes to including more molecular information from

fewer species. Our work suggests that multi-species genetic data may be a cost- and time-effective surrogate for genomic data in spatial planning.

Keywords: evolutionary potential, spatial conservation planning, conservation genomics, genetic diversity, Marxan, surrogacy

Introduction

In a rapidly changing environment that is reshaping patterns of biodiversity across land- and seascapes, it is more important than ever to focus conservation efforts on protecting multiple facets of biodiversity, i.e. species, communities, and their evolutionary histories (Carvalho et al., 2010). Landscape-specific evolutionary processes can help identify conservation priority areas that achieve multiple objectives such as representing spatio-temporal patterns of genetic variation, population dynamics, and divergence (Funk et al., 2019, 2012). While patterns of evolutionary variation have been highlighted as an essential biodiversity feature to ensure species' persistence through environmental change (Flanagan et al., 2018; von der Heyden, 2017), there remains limited knowledge on the effectiveness of different molecular metrics at capturing intraspecific evolutionary and adaptive potential (Mittell et al., 2015).

Integrating genetic and genomic variation into conservation planning

Over the past four decades, evolutionary processes have been captured by molecular markers pertaining to a small portion of the genome, in particular mitochondrial DNA sequences (mtDNA) and microsatellite loci (Moritz, 1994; Schlötterer, 2000). However, with the advancement of next-generation sequencing (NGS), genome-wide single nucleotide

polymorphism (SNP) markers are steadily gaining popularity for both model and non-model organisms (Ouborg et al., 2010). Therefore, theoretical calls for including evolutionary processes in conservation decisions are shifting from incorporating genetic (e.g. AFLP: Thomassen et al., 2011; mtDNA: Nielsen et al., 2017; and microsatellite: Beger et al., 2014; Paz-Vinas et al., 2018) to genomic (e.g. SNP) variation (Allendorf et al., 2010; Shafer et al., 2015).

With the advancement of genomic sequencing and the growing number of available molecular markers, it is important to understand the advantages, as well as limitations, unique to each marker type. Molecular markers can be classified as 'genetic', defined here as the sequencing/genotyping of a specific region of the genome, or as 'genomic', defined here as high-throughput sampling of the partial or entire genome (Table 1). Currently, genetic markers, such as microsatellite loci, organelle-specific genes, and nuclear genes (nDNA), make up most of the genetic data available to inform conservation decisions (Lawrence et al., 2019; Schlötterer, 2004; Seeb et al., 2011). Yet, the use of genomic markers is steadily increasing (Corlett, 2017), making more of such data available for conservation. Genetic markers usually consist of few loci, with mitochondrial and chloroplast DNA (mtDNA and cpDNA) sequences only containing DNA inherited via the maternal line. Most genetic markers predominantly reflect neutral patterns (Table 1; Gebremedhin et al., 2009; Kohn et al., 2006), but there is evidence that some regions of mtDNA (Bazin et al., 2006), as well as microsatellite loci (Larsson et al., 2007) can be under selection, either directly or indirectly via genetic hitchhiking, where markers are physically linked to regions under selection.

Comparatively, genomic markers can include thousands to millions of loci, representing a much larger portion of the genome (Table 1; Allendorf et al., 2010; Garner et al., 2016). Genome-wide SNPs are similar to nDNA and microsatellite loci in that they are bi-

parentally inherited, but SNPs better detect low levels of genetic structure at finer-scales than the former (Puritz et al., 2012), and better represent genome-wide diversity (Fischer et al., 2017). SNP datasets also provide an opportunity to identify markers putatively under selection, termed candidate or outlier loci (from here onwards referred to as outlier loci; Supplement 1), an important consideration given that these loci may provide adaptive benefits to populations and species (Mahony et al., 2020; Narum et al., 2013). Even though SNP datasets offer considerably more evolutionary information, biases can be introduced during library preparation, sequencing, and bioinformatic analyses (Kofler et al., 2016; Supplement 1). There are also limitations associated with restriction-site associated DNA sequencing (RAD-Seq) to identify outlier loci (Lowry et al., 2017a), yet this approach is still relevant and widely used (Lowry et al., 2017b; Supplement 1). Nevertheless, uncertainties are also inherent in other biological data types that inform conservation decisions (Kujala et al., 2013), and conservation scientists and managers must account for uncertainty associated with genomic data.

Regardless of marker type, molecular data have the power to contribute a number of metrics to the conservation planning toolbox. Three of the most commonly available, and useful, metrics for conservation are those that describe patterns of genetic differentiation, uniqueness, and diversity (Table 2; Beger et al., 2014). These include fixation indices, or F_{ST}-based metrics, which report levels of intra-population heterozygosity in relation to other populations, and, from a conservation perspective, form the basis for the concept of Evolutionary Significant Units (ESUs; *sensu* Moritz, 1994; Table 2). For genomic data, these metrics can be extended to outlier SNP F_{ST}-based metrics that can help identify different selective pressures amongst populations (Table 2; Funk et al., 2012). Metrics of diversity are also relevant for conservation, as populations with high levels of genetic diversity are

97 expected to exhibit longer persistence, as there is more standing variation for selection to
98 act on (Table 2; Hoffmann et al., 2015; Reed and Frankham, 2003). High genetic diversity
99 also correlates with increased ecosystem functioning and resilience (Ehlers et al., 2008;
100 Wernberg et al., 2018). Metrics of uniqueness, which for example can be measured by the
101 number of private alleles (i.e. alleles that are restricted to single populations), provide
102 further important criteria for conservation planning (Table 2; Nielsen et al., 2017; Paz-Vinas
103 et al., 2018; Slatkin, 1995). The percentage of private alleles/haplotypes in a population can
104 reflect past range expansions/contractions, as well as the amount of contemporary gene
105 flow with other populations (Maggs et al., 2008). Private alleles can inform two main
106 conservation objectives: i) to prioritize areas with high levels of private alleles, as they might
107 act as genetic reservoirs of variation, thus increasing the genetic insurance of the meta-
108 population; or ii) to prioritize areas with low levels of private alleles, as these areas are likely
109 to be well-connected via gene flow, thus ensuring the persistence and functioning of the
110 meta-population. Further, genomic datasets can account for signals of local adaptation by
111 characterizing 'functional outlier loci', where the functionality of the locus is known via
112 genotype-phenotype analyses or expression profiling (Harrisson et al., 2014). However,
113 identifying 'true' outlier loci is challenging, potentially leading to the inclusion of false
114 positives (Hoban et al., 2016; Lotterhos et al., 2017; Lotterhos and Whitlock, 2015;
115 Supplement 1), and in many non-model species the functional relevance of outlier loci
116 remains unknown.
117
118 *Investigating the surrogacy of genetic for genomic data within conservation planning*
119 A key concern within conservation science is to determine how much information is
120 required to meet conservation targets defined *a priori*, as well as the trade-offs associated

121 with including broader versus finer scale biodiversity features (Wilson et al., 2007).
122 However, this question is rarely extended to molecular information (Goodwin et al., 2016),
123 despite the potential advantages of these metrics to identify areas of evolutionary
124 importance and resilience. While genomic approaches are well-suited to describe the
125 evolutionary potential of natural populations, such as populations distinguished by highly
126 differentiated loci that signal selection in response to local conditions (Funk et al., 2019), the
127 number of available genomic datasets for conservation is lagging behind those using
128 traditional markers (Ouborg et al., 2010; Seeb et al., 2011). In many parts of the world,
129 especially developing countries where conservation action is needed the most (Wilson et al.,
130 2016), the only available multi-species molecular data will likely be genetic. Thus, it is
131 important to understand a) how spatial prioritizations change when including genetic or
132 genomic metrics and b) whether genetic metrics can adequately represent highly
133 differentiated areas (indicating unique evolutionary potential) identified by genomic
134 markers. In this study, we utilize genetic and genomic data generated for multiple marine
135 species to explore the applicability of genetic metrics as surrogates of genomic variation
136 within an empirical conservation planning framework.
137
138 **Methods**
139 While genomic markers are considered the ideal approach to identify loci under selection,
140 genetic approaches may inadvertently also be able to capture patterns of selection for
141 conservation purposes (Bridge et al., 2016). To test how well different molecular
142 approaches capture selective signals in a conservation planning framework, we utilized
143 available datasets previously generated by Mertens et al. (2018) and Nielsen et al. (2018).
144 Here we took advantage of these unique datasets, which were sampled from the same six

145 sample sites for both genetic and genomic approaches, making them comparable in spatial
146 planning analyses (Supplement 2). Molecular metrics were derived from previous studies
147 including mtDNA data for five species (Granular limpet - *Scutellastra granularis*, Cape urchin
148 - *Parechinus angulosus*, Cushion star - *Parvulastra exigua*, Topshell winkle - *Oxystele tigrina*,
149 and Super klipfish - *Clinus superciliosus*; Mertens et al., 2018), and SNP data for two of these
150 species (*S. granularis* and *P. angulosus*; Supplement 3; Nielsen et al., 2018). These species
151 are characterized by different niches, life-history traits, reproductive strategies and larval
152 duration periods (Mertens et al. 2018), and as such represent the species and functional
153 diversity of rocky shore ecosystems of the study region. The mtDNA data consists of the
154 cytochrome oxidase 1 (CO1) gene for the invertebrates and the control region for *C.*
155 *superciliosus*, with total numbers of individuals collected ranging between 128 (*C.*
156 *superciliosus*) and 197 (*S. granularis*). *Parechinus angulosus*, *C. superciliosus* and *P. exigua*
157 show varying levels of population divergence, regardless of the mtDNA marker used,
158 whereas *S. granularis* and *O. tigrina* appear panmictic along the study region.
159 Due to cost restraints, SNP datasets could only be generated for two species, with *P.*
160 *angulosus* and *S. granularis* chosen as these display the highest and lowest levels of
161 population divergence using mtDNA data. Equal numbers of individuals were collected per
162 species (n = 40) for the same sampling points along the South African west coast and a
163 pooled RAD-seq approach (Supplement 1) was used to calculate metrics of population
164 diversity and divergence (Kahnt et al., 2018; Nielsen et al., 2018; Phair et al., 2019). The SNP
165 data, consisting of ~ 8 000 SNPs for *P. angulosus* and ~55 000 SNPs for *S. granularis,* showed
166 levels of population divergence, and high levels of private and outlier SNPs within the
167 northern populations for both species (Nielsen et al. 2018).
168

169 *Empirical spatial prioritization analyses*

170 We chose to include metrics of both diversity and uniqueness (Table 2) and therefore
171 included nucleotide diversity (π) and percentage of private alleles, respectively, for both
172 mtDNA and SNP markers. In addition, the genomic dataset allowed us to include one metric
173 of putative selection (measured as the percent of outlier SNPs).

174 To compare the prioritizations of different molecular metrics, we utilized the
175 decision-support tool Marxan (Ball et al., 2009), which uses a simulated annealing algorithm
176 to identify sets of sites that meet given conservation targets at minimum costs. We included
177 the rocky shore and mixed shore habitat types as our domain, which were divided into 3 x 3
178 km hexagonal planning units. As conservation planning efforts often have to consider an
179 array of socio-economic pressures in balance with meeting biological targets, we included
180 an 'opportunity cost' information in all scenarios. The Marxan algorithm uses cost to
181 prioritize planning units that capture the greatest amount of each biological feature, whilst
182 keeping the total cost of the prioritized set of sites at a minimum (Margules et al., 1988). We
183 applied opportunity cost data derived from Majiedt et al. (2013), which is based on 27
184 marine pressure factors combining extractive practices and marine resource uses, and
185 ranging from commercial fishing, shipping, diamond and titanium mining, to coastal
186 development. This dataset was specifically assembled for the South African west coast and
187 is thus representative of the economic activities of the region.

188 As a baseline scenario, we included five rocky shore substrate types (boulder,
189 exposed, very exposed, sheltered and mixed coast; Sink et al., 2012) as conservation
190 features, to which all molecular metrics were subsequently added (Table 3). Following best
191 practice for generating 'genetic surfaces' (Murphy et al., 2008; Vandergast et al., 2011), we
192 interpolated the point values over the planning region using the Inverse Distance Weighting

193 (IDW) algorithm in ArcGIS v.10.3.1 (Desktop, 2011). We reclassified the IDW raster layers
194 with the 'reclassify' tool in ArcGIS, normalizing the continuous point values of each metric
195 into three equal-interval bins or classes: low, medium, high. For each species, each metric
196 was a single feature with three different levels pertaining to the low, medium and high
197 classes derived from the range of values specific to that metric for that species. We chose to
198 specifically explore the conservation objective of protecting the evolutionary potential
199 (Table 2), by selecting a range of conservation targets (i.e. 20-80%) for solely the high-
200 ranking classes of each molecular feature.

201 We ran five spatial prioritization scenarios to test the effect of increasing molecular
202 information (Table 3): coastal habitat types (*base*), mtDNA diversity and uniqueness metrics
203 for two species (*mt2*), or five species (*mt5*), two SNP metrics (diversity and uniqueness) for
204 two species (*snp2*), and three SNP metrics (diversity, uniqueness, and selection) for two
205 species (*snp3*). We did not run a prioritization based solely on putative outlier SNPs as the
206 potential function of such SNPs remains unknown (Table 2; Harrisson et al., 2014). For each
207 scenario, we ran Marxan with default parameters, a boundary length modifier of zero, and
208 100 repeats to account for variability within the conservation solutions. To compare the
209 conservation solutions, we conducted hierarchical clustering using Euclidean dissimilarities
210 from the selection frequencies (i.e. the number of times the unit was selected out of 100
211 runs) per scenario in RStudio v.1.1.423 (Team, 2015).

212 To assess how well each conservation scenario captured putative selection patterns
213 of *P. angulosus* and *S. granularis*, we calculated a population-specific Selection Index in a
214 similar manner as the Population Adaptive Index described by Bonin et al. (2007b). We
215 created an allele frequency distribution for each outlier SNP, and if in a specific population,
216 the outlier was in the 95th percentile of the overall allele frequency distribution, then it was

counted towards the Selection Index of that specific population. The Selection Index was interpolated across the entire planning region employing the IDW technique. We calculated the Selection Index captured per scenario by multiplying the Marxan selection frequency by the Selection Index of each planning unit, which was summed across all planning units per scenario.

To test the effect of increasing species, we ran another set of scenarios (Table 3): mtDNA data from one (*mt1r*), two (*mt2r*), three (*mt3r*), and four species (*mt4r*), ran five separate times each, including randomly selected species. We compared the total Selection Index captured by these scenarios as above.

Results

Spatial prioritization analyses

The scenarios comparing different amounts of molecular information showed a variety of spatial priorities, with the two most similar being *mt5* and *snp3*, followed by *mt2* and *snp2*, and the baseline being the most distinct (Fig. 1). Most of the conservation targets displayed the same patterns between scenarios, with the exception of the 20% target, which showed *mt5* as the most divergent scenario, and *mt2* and *snp3* being the most similar (Fig. 1).

Performance of conservation objectives in capturing local selective signals

When comparing the Selection Index between scenarios varying in the amount of molecular information, the two worst performing scenarios were *base* and *snp2*, with both only capturing a small portion of the *P. angulosus* Selection Index (Fig. 2). In contrast, the two best performing scenarios were *mt5* and *snp3*, which consistently had the highest Selection Index for both species across the conservation targets (Fig. 2).

241 The scenarios comparing molecular data from different numbers of species show a
242 positive relationship between the number of species included and the Selection Index for *S.*
243 *granularis*, but the Selection Index captured plateaus around three species for *P. angulosus*
244 for each target coverage (Fig. 3)
245
246 **Discussion**
247 This study offers the first experimental comparison of multi-species genetic and genomic
248 datasets within spatial conservation prioritizations. We present initial evidence of genetic
249 markers acting as adequate surrogates of genomic data in capturing evolutionary potential
250 in spatial plans (Fig 1, Fig. 2). We find that including measures from either putatively neutral
251 or outlier genomic regions will change conservation solutions (Fig. 1), highlighting the
252 potential of NGS techniques, specifically the identification of outlier loci, to enhance reserve
253 designs (Ouborg et al., 2010). Our results also show that habitat types, single-species
254 genetic data, and multi-species neutral genomic data inadequately capture evolutionary
255 potential (Fig. 2, Fig. 3). Broadly, the findings suggest a trade-off between the number of
256 species and the amount of molecular information included (Fig. 1, Fig. 2). This has
257 implications for spatial conservation planning, as genetic data may in many cases be more
258 economical to generate compared to NGS (Langmead and Nellore, 2018), and is readily
259 available, especially for a wider array of species (Lawrence et al., 2019; Seeb et al., 2011).
260 Our results also illustrate how spatial priorities are highly dependent on the number
261 of species included regardless of conservation target (Fig. 3), and thus multi-species
262 approaches are essential for conservation prioritizations with genetic data (Fig. 2, Fig. 3;
263 Paz-Vinas et al. 2018). This is most likely driven by differences in ecological traits and
264 evolutionary histories of species, where co-distributed and even closely related species can

display highly divergent patterns of spatial genetic variation (Borsa et al., 2016; Papadopoulou and Knowles, 2016). As umbrella- and surrogate-species show inconsistent efficiency in representing species distributions and assemblages, as well as genetic patterns (Carvalho et al., 2010; Ponce-Reyes et al., 2014), basing conservation plans on multi-species datasets should increase the likelihood of protecting complex evolutionary histories within a region (Nielsen et al. 2017; Paz-Vinas et al. 2018).

Potential surrogates of genomic selective signals in spatial conservation planning

From a spatial planning perspective focused on capturing evolutionary potential, we find that including less molecular information (i.e. a single mtDNA locus) for several species can effectively represent putative adaptive variation identified from vastly more genomic information (i.e. thousands of SNP loci) from fewer species (Fig. 1, Fig. 2). The results also show that the overall Selection Index increased with the number of species included (Fig. 3), suggesting that including genetic variation for multiple species may inadvertently capture local selective pressures. However, this pattern was mainly seen in *S. granularis* (Fig. 3), which highlights how the signals of selective pressures are likely to be species-specific. As spatial plans may only include genomic signals from one or a few species that are likely species-specific, it is essential that surrogates of selection are included for additional species to achieve multi-species complementarity within this biodiversity feature.

Our findings corroborate those of Hermoso et al. (2016), who found that species distribution patterns of 46 freshwater fish were effective surrogates for the genetic patterns of four individual fish species. Furthermore, Wright et al. (2015) found that species richness patterns of over 2 500 species mirrored the patterns of genetic diversity of 11 rocky shore species, suggesting that species- and molecular-level patterns may be a product of similar

processes (Vellend, 2005). Conversely, Paz-Vinas et al. (2018) showed that conservation solutions based on the co-occurrence of high numbers of species did not capture the intraspecific genetic diversity of a set of six fish species. Species richness patterns have also been shown to insufficiently represent phylogenetic diversity (Pio et al., 2011), supporting the need to incorporate fine-scale molecular data to adequately conserve evolutionary patterns.

In addition to using species-level data as surrogates of genomic variation, abiotic factors may also be potential proxies of local selection in spatial conservation plans. For example, when species distribution data is incomplete, partitioning reserves along biophysical gradients will incidentally capture a representative amount of areas pertaining to intraspecific evolutionary potential (Bridge et al., 2016; Carvalho et al., 2010). Further, Hanson et al. (2017) found that environmental features are adequate surrogates of adaptive variation in AFLPs across ten alpine plant species. Yet the effectiveness of selecting environmentally diverse areas to incidentally capture genomic adaptive potential is still largely unexplored, especially within the marine environment.

A way forward comparing molecular approaches in conservation planning

Capturing multi-species genomic signals with genetic metrics provides exciting opportunities to utilize available genetic datasets within conservation planning efforts. Our study provides a baseline for comparing genetic and genomic approaches in capturing evolutionary potential, however further work is required to truly expand the results obtained here to other natural systems. As our study domain is over a relatively small region, it is crucial to test whether similar results are found over larger scales and across different environmental systems. While this study would benefit from additional sample sites, we were restricted to

313 using genetic and genomic datasets from the same locations, as different sample sites
314 would influence conservation outputs and bias comparisons between data types. Our work
315 also included genetic data from mtDNA loci, leaving the ability of other genetic metrics to
316 capture genomic signatures unexplored. For example, microsatellite-derived metrics will
317 likely be more effective surrogates of genomic datasets as they are bi-parentally inherited
318 and show higher intraspecific variability, although this also remains to be formally tested.
319 Furthermore, our SNPs were obtained from a pooled, reduced representation
320 sequencing approach, which is increasingly being used to generate allelic frequencies for
321 populations (Kurland et al., 2019). This methodology has several merits, namely a cost-
322 effective increase in the number of individuals that can be sequenced per population, which
323 can increase the accuracy of allele frequencies, but also a few limitations, such as low
324 frequency alleles and portions of the genome outside of restriction cut sites may be
325 undetected (see Supplement 1 for further details). However, it was recently found that
326 abundant/fine-scale sampling has greater influence on genomic patterns than more in-
327 depth genomic sequencing (D'Aloia et al., 2020), and thus we chose to include more sample
328 sites and individuals per sample site, rather than more detailed genomic information per
329 individual. To further strengthen our findings, additional efforts comparing trade-offs
330 between traditional genetic markers and whole-genome sequencing data in conservation
331 planning scenarios is recommended.
332 Our analyses were focused on comparing genetic and genomic metrics of diversity
333 rather than differentiation, and as such we did not include scenarios based on genetic
334 clusters, although it is essential that these approaches are compared in their efficiency in
335 capturing putatively neutral and adaptive population clusters. Several studies have found
336 similar differentiation patterns between the two molecular marker types (e.g. Benestan et

al., 2015; Dowle et al., 2015; Fernández et al., 2016; Ford et al., 2015), while, alternatively, several others have identified fine-scale structuring with genomic data where genetic data did not (e.g. Blanco-Bercial and Bucklin, 2016; Castellani et al., 2012; Dierickx et al., 2015; Maroso et al., 2016). Therefore, a comprehensive analysis should be conducted to understand if genomic-derived clusters significantly alter conservation scenarios, in order to better assess the trade-offs between the two marker types.

Assessing different marker types, population differentiation metrics, and broader study regions will further resolve the trade-offs between molecular information and species included into conservation plans. In addition, while this study compares molecular metrics of differentiation, uniqueness, and diversity, we recognize that these are not the only molecular features of conservation importance. Many others, including estimates of effective population size (Frankham et al., 2014), demographic change (Garza and Williamson, 2001), inbreeding (Marshall et al., 1999) and hybridization (Buonaccorsi et al., 2005), as well as migration estimates (von der Heyden et al., 2008) may all be relevant measures to support conservation objectives in spatial planning.

Overall, this study highlights how genomic signals of evolutionary potential in two species can be adequately represented by putatively neutral genetic variation across five species, even at low conservation targets. We offer preliminary evidence that genetic data may be a cost- and time-effective surrogate for genomic data when seeking to conserve putative adaptive variation, but ultimately more work is needed to confirm these results within larger conservation settings.

Appendix A. Supplementary data

A comparison of different genomic sequencing and outlier detection methodologies (Appendix S1), as well as sample sites (Appendix S2) and sampling information (Appendix S3) on datasets used within the spatial analyses are available online. 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.

Declaration of Competing Interest

There are no perceived actual or potential conflicts of interest including any financial, personal or other relationships with other people or organizations that could inappropriately influence, or be perceived to influence, our work. All funding agencies are acknowledged.

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670

671 **Table 1.** Comparisons of genetic and genomic approaches, including markers available, as
672 well as marker-specific pros and cons.

Data type	Marker characteristics	Markers	Pros	Cons
Genetic data	Maternally or bi-parentally inherited Dominant or co-dominant One or a few loci	Amplified Fragment Length Polymorphisms (AFLPs), chloroplast DNA (cpDNA), mitochondrial DNA (mtDNA), nuclear DNA (nDNA), microsatellites	Standardised analyses, less researcher-based bias, easy to interpret Lower costs as fewer markers sequenced, requires greater number of individuals sampled in each population	Less power to detect genetic differentiation Usually detects historical measures of diversity (unless microsatellites) Generally not capable of detecting adaptive variation (unless indirectly – e.g. genetic hitchhiking in microsatellites)
Genomic data	Bi-parentally inherited Co-dominant Potentially thousands of loci	SNPs, outlier SNPs	Potentially provides greater resolution of population structure, demographic processes etc., due to the availability of thousands of markers for both neutral and adaptive loci	Data analysis often requires training in command-line or outsourcing of bioinformatic analyses Lack of standardized analyses Outlier detection methods prone to false positives

673

Table 2. Definitions of genetic and genomic features, their conservation relevance and how they contribute towards spatial planning by capturing either spatial-temporal processes or evolutionary potential.

Molecular features	**Conservation relevance**	**Potential conservation objectives**
Measure: differentiation		
- Genetic & Genomic: Local F_{ST} Measures how much the genetic diversity of a population differs from the mean of all other populations combined - Genetic & Genomic: Pairwise F_{ST} Measures how much the genetic diversity differs between two populations	Low distinctiveness indicates that a site is connected to others by high levels of gene flow, meaning it can increase resilience by supplementing individuals to the meta-population High distinctiveness indicates low levels of gene flow, meaning it might have lower resilience to stochastic change due to it not being connected to the meta-population. It could also indicate local adaptation or recent bottleneck events. In this case, a site can potentially play an important role in increasing the resilience of the meta-population by harboring unique alleles that can be advantageous in future environmental changes	Avoid low differentiation regions (prioritize evolutionary potential) Protect low differentiation regions (prioritize connectivity) Give highly differentiated regions conservation priority (prioritize evolutionary potential) Prioritize connected regions as pairs instead of as individual sites (prioritize connectivity)
Measure: diversity		
- Genetic: Haplotype diversity	Low diversity may indicate small effective population sizes, and a lower likelihood of adaptation from standing variation. These sites are at greater risk to inbreeding depression and stochastic change	Protect high diversity regions (prioritize evolutionary potential)

Probability that two randomly selected individuals differ in their haplotypes Unlike nucleotide diversity, which is site specific, haplotype diversity is calculated from all populations, and therefore incorporates gene flow	High diversity is beneficial for long-term persistence and adaptation as there is more 'raw material' for selection to act on. These regions are assumed to be more resilient to environmental change	
- Genetic & Genomic: Nucleotide diversity Average number of nucleotide differences per genomic site, between randomly chosen SNPs from within a population		
Measure: uniqueness - Genetic: Private haplotypes/alleles Haplotypes/alleles unique to a single geographic area - Genomic: Private SNPs Neutral loci that are unique to particular areas. They are different to outlier loci (see below), as they are not under selection	Low levels of private alleles indicate that the region is connected to others by high levels of gene flow, meaning it can increase resilience by supplementing individuals to the meta-population A high percentage of private alleles could indicate low levels of gene flow, meaning lower resilience to stochastic change. High levels of private alleles could also denote local adaptation or recent bottleneck events. In this case, the region can potentially play an important role in increasing the resilience of the meta-population by harboring unique alleles that can be advantageous to future environmental changes	Protect regions with few private alleles (prioritize connectivity) Protect unique regions with many private alleles (prioritize evolutionary potential)

Measure: selection / evolutionary potential - Genomic: Non-functional outlier loci richness Loci that are statistically significantly different from other regions of the genome. The function roles of the loci are often unknown	A high percentage of outliers indicates that selection is occurring on individuals in that area. It may be assumed that the selection leads to increased fitness and that this selection will continue to benefit the individual fitness under future environmental conditions	Protect populations with high levels of outlier loci (prioritize evolutionary potential)
Measure: selection / evolutionary potential - Genomic: Non-functional outlier loci structure Genetic clusters that are inferred from differentiation of outlier loci. The clusters can be displayed geographically to illustrate where genetic breaks occur	Different genetic clusters are likely to be under different selective regimes; therefore, each cluster is assumed to have its own unique evolutionary trajectory. Each cluster can potentially act as genetic insurance for the meta-population	Aim to protect a percentage of each cluster in an adaptive landscape (prioritize evolutionary potential)
Measure: selection / evolutionary potential - Genomic: Functional outlier loci Loci that are shown to under selection through experiments or through strong correlations with environmental	If environmental feature(s) driving selection and/or functional role of the outliers are known, these features would indicate which regions are of conservation importance This scenario could also be of importance for human-mediated adaptive assistance. It is also important to note that this scenario is still quite rare and mainly confined to model organisms	Protect areas in which environmental features are driving known adaptation Protect areas where known adaptive genes occur

variables. The genes corresponding to the loci, as well as their functional roles, are often identified

Assist un-adapted sites with breeding programs

Table 3. The various prioritizations run in Marxan, with their included biodiversity features and species (CS = *Clinus superciliosus*, PA = *Parechinus angulosus*, PE = *Parvulastra exigua*, OT = *Oxystele tigrina*, SG = *Scutellastra granularis*)

Scenario I.D.	Biodiversity features compared	Species included
	Scenarios increasing in molecular data	
base	Five different habitat types; no genetic/genomic system features	NA
mt2	Diversity and uniqueness metrics from mtDNA markers for the two species with genomic data	PA, SG
mt5	Diversity and uniqueness metrics from mtDNA markers for five species	All
snp2	Diversity and uniqueness metrics from putatively neutral SNPs for the two species with genomic data	PA, SG
snp3	Diversity, uniqueness, and selection metrics for putatively neutral and highly differentiated SNPs for the two species with genomic data	PA, SG
	Scenarios increasing in species	
mt1r	Neutral metrics (diversity and uniqueness) from mtDNA markers for one randomly chosen species	All
mt2r	Neutral metrics (diversity and uniqueness) from mtDNA markers for two randomly chosen species	PE, CS PA, SG OT, PE OT, SG PE, SG
mt3r	Neutral metrics (diversity and uniqueness) from mtDNA markers for three randomly chosen species	PE, OT, SG CS, OT, PA CS, PA, PE CS, SG, PA PE, SG, PA
mt4r	Neutral metrics (diversity and uniqueness) from mtDNA markers for four randomly chosen species	PE, SG, CS, PA SG, OT, CS, PA CS, PE, SG, OT SG, OT, PE, PA PE, PA, OT, CS

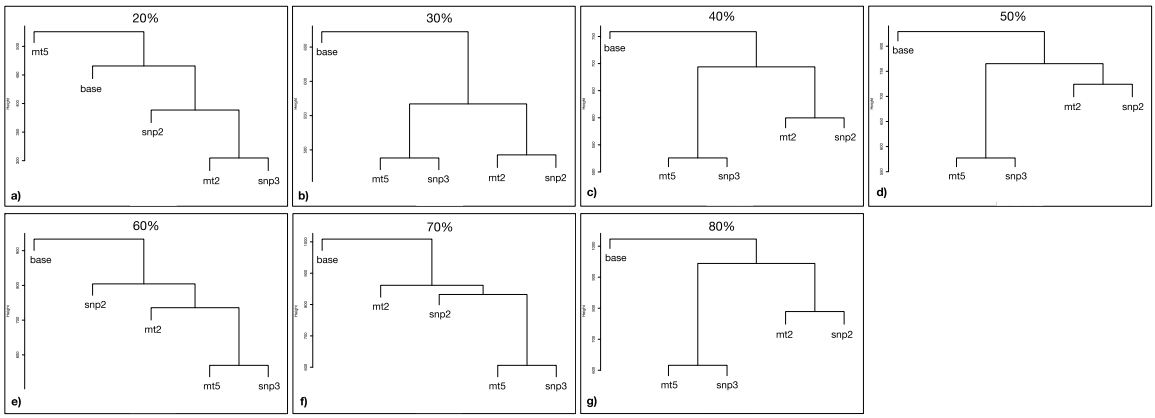

Figure 1. Hierarchical clustering dendrograms illustrating the similarities between scenarios for conservation targets ranging from 20-80% of each biodiversity feature.

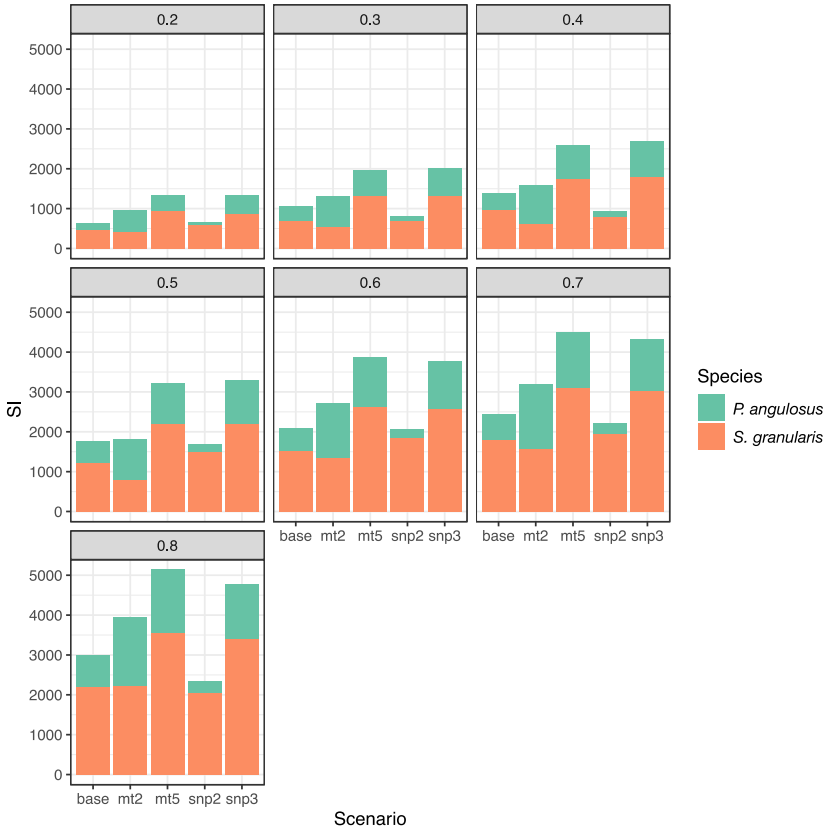

Figure 2. The Selection Index (SI) captured per species for genetic and genomic scenarios (see Table 3 for scenario explanations), shown for targets ranging from 20-80% (0.2-0.8) of each biodiversity feature.

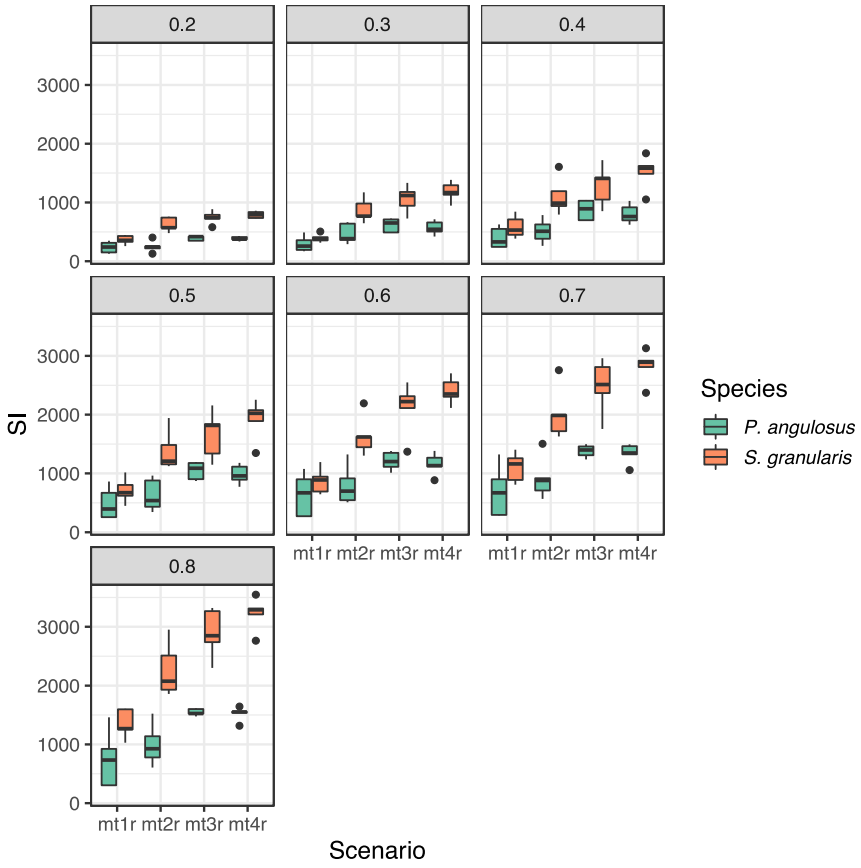

Figure 3. The Selection Index (SI) captured per species for genetic scenarios with varying number of species (see Table 3 for scenario explanations), shown for targets ranging from 20-80% (0.2-0.8) of each biodiversity feature.

Supplementary data

Appendix S1- The definitions, as well as advantages and disadvantages, of the methods used obtain genomic inferences in the present study, compared to other possible molecular approaches. This is not an exhaustive list of molecular methodologies for conservation, but is rather restricted to those relating to next generation sequencing (NGS) methods for DNA-based sequencing, pertaining to sequencing and identification of outlier loci, and some considerations with regards to their use for conservation. The methods used to generate the genomic data within the present study are indicated in bold. It should also be noted that even using the NGS techniques with lowest costs/highest uncertainties, the amount of genomic information, and sequencing costs, are still substantially greater than traditional genetic techniques (see Table 1 for genetic and genomic comparisons).

1: Allocation of samples for sequencing				
Method	Definition	Advantages	Disadvantages	References
Individual sequencing	Individuals have distinct barcodes and are sequenced with other barcoded individuals	Individual haplotypes/genotypes are available Can conduct assignment tests, and calculate clonality, relatedness, inbreeding coefficients, and linkage disequilibrium	High sequencing costs, likely leading to trade-offs between individuals and sample sites sequenced, as well as the depth of coverage	Anderson et al. (2014) Dorant et al. (2019) Ferretti et al. (2013)

Pooled sequencing (Pool-seq)	Individuals are pooled into a single sample (usually pertaining to a sample site/population). Each pooled sample receives a barcode and is sequenced with other barcoded samples	Low sequencing costs, making it feasible to sample many locations and individuals per location, as well as making NGS available for many groups in developing regions, especially when combined with a reduced-representation sequencing type (i.e. Probe-/RAD-seq detailed below) Accurate allele frequencies for outlier detection methods, as the number of sequenced individuals is usually higher per population than individual sequencing	Individual genotypes and inferences from them are unavailable Need accurate equimolar pooling across individuals to best attain allelic variance. Errors from unequal representation between individuals in a sample can be reduced by large pool sizes and removal of PCR duplicates Contamination and sequencing biases can occur on the population rather than individual level Low frequency alleles will be lost in bioinformatic stages aimed at filtering sequencing artefacts	Gautier et al. (2013) Hivert et al. (2018) Inbar et al. (2020) Kofler et al. (2016) Kurland et al. (2019) Lynch et al. (2014) Rellstab et al. (2013) Schlötterer et al. (2014) Tilk et al. (2019)
2: Sequencing type				
Whole genome sequencing (WGS)/ Whole genome resequencing (WGR)	Portions of the genome (termed 'reads') are sequenced and either: 1) assembled to create a genomic sequence for the first time (WGS), or 2) mapped onto an existing reference genome to compare genomic variability between individuals/populations (WGR)	Extensive and complete genomic information One single continuous genomic sequence, allowing for no gaps in the data Increased power for statistical analyses	Exceedingly high costs, especially when using individual sequencing at high coverage across the genome. To counteract the high costs, many studies use Pool-seq WGS or low-coverage WGS (lcWGS) Many research questions, and inferences for conservation (such as population structure and diversity) do not require the entire genomic sequence, and thus the high sequencing costs can be avoided by	Andrews et al. (2016) Andrews and Luikart (2014) Carpenter et al. (2013) Catchen et al. (2017) da Fonseca et al. (2016)

			using reduced-representation sequencing instead	Díaz-Arce and Rodríguez-Ezpeleta (2019) Fuentes-Pardo and Ruzzante (2017) Goodwin et al. (2016) Graham et al. (2020) Lowry et al. (2017a, 2017b) Mckinney et al. (2017) Meek and Larson (2019) Narum et al. (2013) Nielsen et al. (2011) Reitzel et al. (2013) Rowe et al. (2011) Teer and Mullikin (2010)
Probe-based/exome capture sequencing	The complexity of the genome is reduced by pre-selecting genomic regions (such protein coding regions, termed 'exons'), and using a DNA probe to target the regions of interest for sequencing. These regions are mapped onto an existing reference genome	Lower costs than WGS/WGR Provides high depth and uniformity of coverage within the designated sequence regions The precise, targeted nature of probe-based sequencing can be beneficial when DNA is degraded Can be used to assess epigenetic modifications (which affect how genes are expressed in the genome)	The development of panels for capture leads to increased costs and time spent on preparation for sequencing Designated sequence regions need to be known *a priori,* making it unsuitable for many non-model organisms which lack any prior genomic information (but see Puritz and Lotterhos, 2018) May not be suitable to for exploratory questions regarding genome-wide evolutionary processes	
Restriction site-associated sequencing (RAD-seq)*	The complexity of the genome is reduced by using restriction enzymes to cut out regions throughout the genome (both coding and non-coding). The areas adjacent to the cut sites are then sequenced. The sequenced fragments can be assembled *de novo*, or mapped onto an existing reference genome	Low costs allow for sequencing of multiple individuals/populations, and at higher coverage. It may also be the most feasible method for smaller research groups, especially within developing countries, to perform genome-wide studies No genomic information is needed *a priori*, making it suitable for non-model organisms, and with *de novo* genome assembly Flexibility of restriction enzymes make it easily scalable, sequencing few loci at high coverage or more loci at low coverage	Possibility of mutations at restriction sites leading to ineffective cutting of fragments (i.e. allele dropout) Sequence amplification during library preparation can lead to unequal duplication of one allele over another within an individual. These 'PCR duplicates' can however be identified and removed during bioinformatic processing The length of the areas adjacent to the cut sites (i.e. the sequenced fragments linked to these sites) varies both between individuals and species, meaning that the portion of the genome sequenced can be more or	

			less incomplete depending on the level of linkage disequilibrium	
3: Outlier detection				
Genetic–environment associations (GEAs)	The variance in allele frequencies is statistically compared with the variance with environmental features predicted to act as selective pressures. Thus, loci which have allele frequencies strongly associated with an environmental variable are identified as outliers	Can detect signals of selection which do not necessarily lead to high differentiation between populations Multivariate GEAs (specifically constrained ordinations) may be more powerful in detecting weak, multilocus selection signatures	Genomic sample sites need to cover the entire environmental gradient Requires high quality environmental data, and results may differ depending on the environmental data included A high rate of false negatives may occur if the direction of past population expansion mirrors the environmental gradient Results have been shown to differ between outlier detection models (Dalongeville et al., 2018; Forester et al., 2017)	Beaumont (2005) Bierne et al. (2013) Booker et al. (2020) Dalongeville et al. (2018) Foll and Gaggiotti (2008) Forester et al. (2017) Grummer et al. (2019)

Differentiation/F_{ST}-based	F_{ST} is a commonly used measure of population differentiation. F_{ST} – based outlier tests are built on the concept of neutral SNPs being affected in a similar manner by processes such as gene flow and genetic drift, while outlier SNPs will be affected in a distinct manner by the process of selection. Outliers are thus selected from loci which have significantly high (indicating divergent selection) or low (indicating balancing selection) F_{ST} values	Does not require high quality environmental data or large number of genomic sample sites Outliers can be identified as either under balancing or divergent selection	Cannot test specific hypotheses as to which environmental selection pressures are acting on outlier loci May not perform well when there are exceedingly high levels of selection biasing the baseline F_{ST} variation Neutral variation is increased when demographic processes occur within a linear fashion, which may lead to high rates of false positives Results have been shown to differ between outlier detection models (Lotterhos and Whitlock 2015; Narum and Hess 2011)	Helyar et al. (2011) Lotterhos and Whitlock (2015) Luikart et al. (2003) Narum and Hess (2011) Rellstab et al. (2015)

* There is a plethora of RAD-seq methods, which are discussed in detail within Andrews et al. (2016). The RAD-seq method used to obtain the data within the present study was a paired-end ezRAD approach (sequenced on the Illumina Mi-seq platform), which was selected as it does not rely on a PCR step to amplify sequences during library preparation, its use with Pool-seq has been compared and validated against individual sequencing, and has been shown to produce high quality data for non-model marine invertebrates (Toonen et al., 2013).

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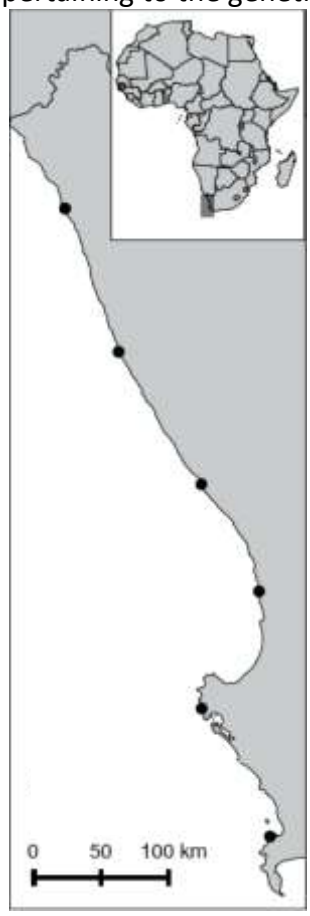
Appendix S2. The six sample sites pertaining to the genetic and genomic material.



Appendix S3. The genetic and genomic datasets, and the associated molecular marker and species, which were included into conservation planning scenarios. The gene region and base pair (bp) length is shown for mtDNA markers, and the number of putatively neutral and adaptive single nucleotide polymorphisms (SNPs) are shown for Pool/RAD-seq SNP markers.

Molecular marker	**Species**	**Reference**
mtDNA cytochrome oxidase I gene, 790 bp	Cape urchin (*Parechinus angulosus*)	Mertens et al. (2018)
mtDNA cytochrome oxidase I gene, 611 bp	Granular limpet (*Scutellastra granularis*)	Mertens et al. (2018)
mtDNA cytochrome oxidase I gene, 473 bp	Tiger topshell winkel (*Oxystele tigrina*)	Mertens et al. (2018)
mtDNA cytochrome oxidase I gene, 651 bp	Cushion star (*Parvulastra exigua*)	Mertens et al. (2018)
mtDNA control region, 373 bp	Super klipfish (*Clinus superciliosus*)	Mertens et al. (2018)
RAD-seq SNPs (55 375 neutral* + 34 outlier SNPs)	Granular limpet (*Scutellastra granularis*)	Nielsen et al. (2018)
RAD-seq SNPs (8 378 neutral* + 8 outlier SNPs)	Cape urchin (*Parechinus angulosus*)	Nielsen et al. (2018)

*refers to putatively neutral SNPs