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Contributed Paper

Incorporating putatively neutral and adaptive genomic data into marine conservation planning

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Abstract: The availability of genomic data for an increasing number of species makes it possible to incorporate evolutionary processes into conservation plans. Recent studies show how genetic data can inform spatial conservation prioritization (SCP), but they focus on metrics of diversity and distinctness derived primarily from neutral genetic data sets. Identifying adaptive genetic markers can provide important information regarding the capacity for populations to adapt to environmental change. Yet, the effect of including metrics based on adaptive genomic data into SCP in comparison to more widely used neutral genetic metrics has not been explored. We used existing genomic data on a commercially exploited species, the giant California sea cucumber (*Parastichopus californicus*), to perform SCP for the coastal region of British Columbia (BC), Canada. Using a RAD-seq data set for 717 *P. californicus* individuals across 24 sampling locations, we identified putatively adaptive (i.e., candidate) single nucleotide polymorphisms (SNPs) based on genotype–environment associations with seafloor temperature. We calculated various metrics for both neutral and candidate SNPs and compared SCP outcomes with independent metrics and combinations of metrics. Priority areas varied depending on whether neutral or candidate SNPs were used and on the specific metric used. For example, targeting sites with a high frequency of warm-temperature-associated alleles to support persistence under future warming prioritized areas in the southern coastal region. In contrast, targeting sites with high expected heterozygosity at candidate loci to support persistence under future environmental uncertainty prioritized areas in the north. When combining metrics, all scenarios generated intermediate solutions, protecting sites that span latitudinal and thermal gradients. Our results demonstrate that distinguishing between neutral and adaptive markers can affect conservation solutions and emphasize the importance of defining objectives when choosing among various genomic metrics for SCP.

Keywords: adaptive genetic variation, climate change, conservation genetics, marine protected area, spatial conservation prioritization

Incorporación de Datos Genómicos Putativamente Neutros y Adaptativos dentro de la Planeación de la Conservación Marina

Resumen: La disponibilidad de los datos genómicos para un número creciente de especies posibilita la incorporación de los procesos evolutivos dentro de los planes de conservación. Los estudios recientes muestran cómo los datos genéticos pueden informar a la priorización de la conservación espacial (PCE) pero tienden a enfocarse más en las medidas de la diversidad y la distinción derivadas principalmente de los conjuntos de datos genéticos neutrales. La identificación de los marcadores genéticos adaptativos puede proporcionar información importante con respecto a la capacidad de las poblaciones para adaptarse al cambio ambiental. Aun así, no se ha explorado el efecto de la inclusión de las medidas basadas en los datos genéticos adaptativos dentro de la PCE y cómo se comparan con las medidas genéticas neutrales de uso más amplio. Usamos datos genómicos existentes sobre una especie de explotación comercial, el pepino de mar gigante de California (*Parastichopus californicus*),

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para realizar la PCE para la región costera de la Columbia Británica (BC) en Canadá. Usamos un conjunto de datos RAD-seq para 717 individuos de la especie *P. californicus* en 24 localidades de muestreo para identificar los polimorfismos de un solo nucleótido (PSNs) putativamente adaptativos (es decir, candidatos) con base en las asociaciones genotipo-ambiente manifestadas con la temperatura del fondo marino. Calculamos varias medidas para los PSNs neutrales y los PSNs candidatos y comparamos los resultados de la PCE con medidas independientes y con combinaciones de medidas. Las áreas prioritarias variaron dependiendo de si se usaron los SNP neutrales o los candidatos y de la medida específica que se utilizó. Por ejemplo, enfocarse en sitios con una frecuencia alta de alelos asociados con agua cálida para fortalecer la persistencia frente al futuro calentamiento prioriza las áreas en la región del sur de la costa. Al contrario, enfocarse en sitios con una alta heterocigosidad esperada en los loci de los candidatos para fortalecer la persistencia frente a la incertidumbre ambiental prioriza las áreas en la parte norte de la costa. Cuando combinamos las medidas, todos los escenarios generaron soluciones intermedias, protegiendo así los sitios que abarcan gradientes latitudinales y gradientes térmicos. Nuestros resultados demuestran que la distinción entre los marcadores neutrales y los adaptativos puede afectar las soluciones de conservación y también enfatizan la importancia de la definición de los objetivos cuando se elige entre varias medidas genómicas para la PCE.

Palabras Clave: área marina protegida, cambio climático, genética de la conservación, priorización de la conservación espacial, variación genética adaptativa

Introduction

Marine protected areas (MPAs) are effective conservation tools because they restrict human activity in their boundaries (Edgar et al. 2014) and can improve population resilience to climate change (Roberts et al. 2017). Nonetheless, designing effective MPAs remains a formidable challenge. A systematic approach to MPA planning can help achieve conservation objectives by incorporating targets for the protection of key biodiversity features and costs associated with conservation actions into an integrated spatial prioritization framework (Margules & Pressey 2000). Spatial conservation prioritization (SCP) thus offers a quantitative approach to select cost-effective priority sites for inclusion in protected areas (Moilanen et al. 2009) and has been applied to delineate optimal MPAs for various objectives, including fisheries management, preservation of marine biodiversity, and mitigation of climate change threats (Wilson et al. 2020).

Genetic information can be used to ensure that evolutionary patterns are also represented in conservation planning (Funk et al. 2012; von der Heyden 2017; Xuereb et al. 2019). Specific advances in marine spatial planning include developing frameworks to incorporate genetic diversity and distinctness in SCP (Beger et al. 2014) and shifting from single-species to multispecies conservation targets (Nielsen et al. 2017; Paz-Vinas et al. 2018). However, to date, SCP studies have focused primarily on metrics derived from neutral genetic markers. Neutral genetic data are valuable for considering demographic history and genetic connectivity in conservation decision-making, but they do not capture patterns of selection. The potential for adaptive genomic markers to represent such patterns of selection and inform conservation actions has been proposed (Funk et al. 2012; von der Heyden 2017; Flanagan et al. 2018), but adaptive markers are rarely explicitly integrated into SCP (but see Hanson et al. [2017]). Protecting adaptive genetic variation can have large effects on future adaptation and long-term persistence of marine populations experiencing (or that are predicted to experience) unfavorable conditions due to climate change and other stressors (Bay & Palumbi 2014; von der Heyden 2017).

Metrics used in SCP to represent conservation features and the approach for selecting priority areas require careful consideration. Genetic metrics may be calculated as indices of within-population attributes and between-population relationships, both of which may be important for conservation (Beger et al. [2014] lists genetic attributes and associated metrics). Nielsen et al. (2017) used 4 genetic metrics to identify priority areas for 5 intertidal species based on genetic diversity, genetic uniqueness, and genetic distinctness. From a conservation perspective, populations with high genetic diversity may be important sources of standing genetic variation, whereas populations with high genetic uniqueness or distinctness may indicate isolation and thus may be deprioritized for protection (Beger et al. 2014). However, genetically unique or distinct populations may alternatively indicate adaptive divergence and therefore could be important for conservation (Beger et al. 2014; Bay & Palumbi 2014). By assessing divergence with both neutral and candidate adaptive genomic markers, it may be possible to distinguish between these contrasting interpretations of observed patterns (e.g., by determining whether limited connectivity or selection are the underlying processes).

Incorporating genomic data into SCP is not trivial. Our objective was to evaluate how SCP solutions may differ depending on the manner in which genomic data are treated and to develop a framework for considering the spatial distribution of genomic variation in marine conservation planning. We considered how genomic data are summarized using different metrics, the type of

underlying genomic data (putatively neutral or adaptive), and the effect of integrating multiple genomic metrics, all of which are key decisions for SCP. We used the California sea cucumber (*Parastichopus californicus*) in coastal British Columbia (BC), Canada, as a case study. *P. californicus* is harvested for human consumption throughout its range along the Pacific coast of North America. Recent seascape genomic work identified population genetic structure and a subset of genomic markers associated with seafloor temperature, indicating the potential for local adaptation in *P. californicus* populations in BC (Xuereb et al. 2018*a*,*b*), making this a useful system for investigating SCP outcomes with genomic data. We considered how genomic metrics affect SCP outcomes for neutral and candidate adaptive genomic markers; whether solutions differ when SCP considers only neutral genomic markers versus candidate adaptive genomic markers; and how solutions based on integrated scenarios, wherein genomic metrics are combined, compare with solutions based on independent metrics. We sought to expand on previous work incorporating neutral genetic metrics in SCP in marine systems (Beger et al. 2014; Nielsen et al. 2017).

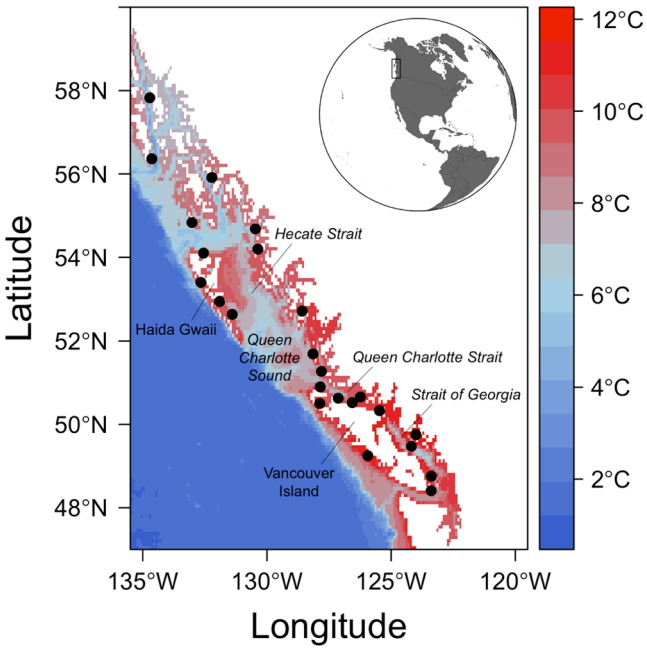

Figure 1. The 24 P. californicus *sampling locations for which neutral and candidate genomic metrics (see Table 1) were calculated and mean bottom temperature for the region (Tyberghein et al. 2012).*

Methods

Data Collection

We used genomic data from 717 *P. californicus* spike-clip samples collected from 24 sites (20–34 samples/site) in coastal BC and southwestern Alaska (Fig. 1) that were published previously by Xuereb et al. (2018*a*). In total, 3699 SNPs were identified from double digest restriction-site-associated DNA sequencing (ddRAD) data. Full details on sample collection, sequencing, filtering, SNP identification methods, and potential advantages and limitations of using RAD-seq data in outlier-detection analyses are described in Xuereb et al. (2018*a*).

We compiled 2 data sets: candidate adaptive SNPs and putatively neutral SNPs. The SNPs identified as adaptive were not experimentally or functionally tested to rigorously demonstrate that they are under divergent selection; thus, we refer to them as candidate genomic markers or candidate SNPs. Such markers are considered valuable for conservation because they are highly divergent and strongly linked with environmental factors and therefore are likely affected by unique evolutionary forces (Allendorf et al. 2010). Candidate SNPs were identified using a genotype–environment association analysis (Xuereb et al. 2018*b*). Specifically, we used a redundancy analysis (RDA) to identify covarying sets of SNPs associated with environmental variables (details in Xuereb et al. [2018*b*]). This analysis detected 59 candidate SNPs associated with bioclimatic variables, 51 of which were associated with mean bottom temperature, which varies latitudinally from ~11°C in the southern portion of our study area to ~6.5°C in the north (Fig. 1). We used the 51 temperature-associated candidate SNPs to calculate the adaptive genomic metrics. The remaining 3648 noncandidate SNPs were deemed putatively neutral and used to calculate the neutral genomic metrics.

To ensure that our SCP results were not biased by detection methods for candidate markers, we also considered candidate SNPs that exhibited the strongest correlations ($r > 0.65$) with mean bottom temperature (16 SNPs); SNPs identified by both RDA and BayeScan (Foll & Gaggiotti 2008) (43 SNPs); SNPs identified by either RDA or BayeScan (71 SNPs); and SNPs identified by BayeScan alone (55 SNPs).

Neutral Genomic Metrics

Metrics computed using neutral genomic markers summarize patterns of genetic variation generated by selectively neutral processes and pertain to demographic considerations in conservation planning. With neutral SNPs, we calculated expected heterozygosity (H_{neut}) and local genetic differentiation (local F_{STneut}) as metrics of genetic diversity and distinctness, respectively (Table 1). We calculated within-site H_{neut} for each sampling location and pairwise F_{ST} with Genodive (Meirmans & Van Tienderen 2004). Local F_{STneut} was calculated for each site as the average of pairwise F_{ST} values between it and all other sites (Foll & Gaggiotti 2006).

Table 1. Summary of genetic metrics used in systematic conservation prioritization.

Conservation feature	*Metric*	*Definition*	*Marker type*	*Reference*
Genetic diversity	expected heterozygosity (H_e)	probability of sampling 2 different alleles within a site	neutral, adaptive	Nei 1973
Genetic distinctness/ uniqueness	local differentiation (F_{ST})	degree to which genetic composition at a given site differs from the mean composition of all sites	neutral, adaptive	Foll & Gaggiotti 2006
	population adaptive index (PAI)	measure of adaptive allele* frequency differences between a given site and mean frequencies across the study area	adaptive	Bonin et al. 2009
Predicted adaptedness	adaptive score (S_{adapt})	proportion of adaptive alleles* averaged across individuals within a given site	adaptive	Manel et al. 2018

**For PAI and S_{adapt}, the adaptive allele in this study refers to the allele that is positively associated with mean bottom temperature across all candidate markers for* P. californicus.

Adaptive Genomic Metrics

Because patterns of variation at neutral loci may not reflect patterns at adaptive loci (Hoffmann & Daborn 2007), metrics of genetic variation at candidate markers may be better proxies for evolutionary potential (von der Heyden 2017). We calculated heterozygosity and local F_{ST} with the 51 candidate SNPs as metrics of adaptive genetic diversity and distinctness (H_{adapt} and $F_{STadapt}$, respectively) (Table 1). We computed two additional metrics based on the assumption that alleles positively associated with bottom temperature are considered adaptive because ocean temperature in the region is predicted to increase (Foreman et al. 2014). The first is the population adaptive index (PAI), which reflects the uniqueness of adaptive genomic diversity in one site compared with all other sites (Bonin et al. 2009; Table 1). The PAI was calculated for each site as the sum of the per-locus absolute difference between the adaptive allele frequency (within site) and the mean frequency of the adaptive allele across all sites. The second metric, adaptive score (S_{adapt}) (Manel et al. 2018) was calculated for each individual as the proportion of alleles positively associated with mean bottom temperature divided by $2C$, where C is the number of candidate SNPs. In our case, individuals with high adaptive scores are expected to have higher fitness under warmer conditions and populations containing a high proportion of these individuals are thus considered to exhibit high potential for local adaptation under a scenario of increasing temperature, which we refer to as predicted "adaptedness." To obtain a within-site value, we estimated the mean adaptive score over all individuals within a site. Correlations among metrics were tested using Pearson's product–moment correlation tests.

Spatial Conservation Prioritization

Following D'Aloia et al. (2017), we divided the BC Continental Shelf into 20 × 20 km planning units (PUs) ($n = 463$). We assumed the entire coastal region is habitat for *P. californicus*. We interpolated values of each metric from the 24 sampling locations across all PUs with an inverse distance-weighting approach carried out with the phylin 1.1.1 package (Tarroso et al. 2015) in R (R Core Team 2018). Although we used all sampling locations for interpolation, we considered only PUs in BC for SCP to restrict the planning exercise to Canada's Exclusive Economic Zone.

We prioritized PUs with the SCP algorithm in the R package prioritizr 4.0.2 (Hanson et al. 2018). The approach used by prioritizr is based on integer linear programing with exact algorithms to find the optimal set of PUs in relation to a specified objective to protect conservation features. Conservation features were the metrics measuring genomic diversity, distinctness or uniqueness, or predicted adaptedness (Table 1) in each PU. We used the minimum set objective (Beger et al. 2014; Nielsen et al. 2017), which aims to identify the smallest set of PUs needed to achieve a given representation target for each conservation feature. We set the feature representation target to protect ~30% of the total number of PUs, which is consistent with the predicted amount of coastline that should be protected to sustain populations (Botsford et al. 2001). To evaluate conservation solutions based solely on genomic marker type (putatively neutral or candidate) and alternative genomic metrics, we held the cost of protecting a PU across the region constant (cost per PU = 1).

We performed additional analyses by varying the PU size (40 × 40 km) and the area-based conservation target (15% and 50%) to ensure that overall SCP solutions were not sensitive to these parameter choices. Finally, we explored the effect of using smaller subsets of neutral markers on spatial planning outcomes by randomly sampling 51 putatively neutral SNPs out of 3648 and performing SCP on the subset with the neutral genomics metrics. We repeated this process 1000 times and evaluated the

selection frequency of each PU across the 1000 resampled neutral data sets.

We included a series of scenarios to explore how genomic data types (putatively neutral or candidate SNPs) and genomic metrics influence SCP outcomes. First, we ran independent scenarios to generate solutions based on each genomic metric separately. Second, we ran combined scenarios to explore how joint consideration of certain metrics shape the optimal solution. We included 6 combinations: neutral diversity and distinctness (H_{neut} and F_{STneut}); adaptive diversity and distinctness (H_{adapt} and $F_{STadapt}$); neutral and adaptive genomic diversity (H_{neut} and H_{adapt}); neutral and adaptive genomic distinctness (F_{STneut} and $F_{STadapt}$); adaptive genomic diversity and predicted adaptedness to future warming (H_{adapt} and S_{adapt}); and predicted adaptedness and adaptive uniqueness (S_{adapt} and PAI). The first and second scenarios allow comparison of solutions based on neutral genomic markers only or adaptive genomic markers only and can indicate whether neutral markers may be used as surrogates of adaptive genetic variation. The third and fourth scenarios were used to compare the choice of metric when integration of information from both neutral and adaptive genomic markers was desirable. We combined H_{adapt} and S_{adapt} (fifth scenario) because these metrics reflect distinct evolutionary processes that may be important for population-level responses to future environmental change. For example, H_{adapt} may be best for variable environmental conditions, whereas S_{adapt} may be best if temperature continues to increase. Finally, we combined S_{adapt} and PAI (sixth scenario) to preserve sites that harbor unique warm-temperature-associated alleles and sites that show a high degree of predicted "adaptedness" under warming conditions. Genomic metric values were scaled between 0 and 1 to ensure all metrics were considered equally in the combined scenarios. For all prioritization scenarios, we used the Gurobi optimization solver (Gurobi Optimization and LLC 2018), as implemented in prioritizr. To compare solutions, we calculated the Jaccard coefficient between each pair of solutions; values close to 1 indicated high similarity in the PUs selected between solutions and values close to 0 indicated low similarity.

Results

Spatial Genetic Patterns

Across the sampled sites, the range of H_{neut} was small (0.111–0.117), and on average pairwise F_{STneut} was low (mean = 0.004) (Table 2). With candidate SNPs, H_{adapt} spanned a wider range (0.072–0.180) than H_{neut}, and there was a significant difference in variance between H_{neut} and H_{adapt} (Levene's test, $F_{1,46} = 298.7$, $p < 0.0001$). Pairwise $F_{STadapt}$ was also significantly higher than F_{STneut} (mean = 0.074; Wilcoxon signed rank test, $Z = -20.362$, $p < 0.0001$) (Table 2). The adaptive score was high (mean = 0.56) (Table 2), meaning that for most sites, over half the 2*51 alleles carried by an individual at the 51 candidate SNPs were positively associated with warm temperatures and are thus expected to be advantageous under future warming conditions. The difference in allele frequency of warm-temperature-associated alleles between a given site and the mean frequency across sites ranged from 0.019 to 0.26, resulting in site-level PAI values between 3.05 and 4.89 (Table 2).

Table 2. Mean and range of variation of the 6 neutral and adaptive genomic metrics over the 24 sites sampled for *P. californicus.**

Genomic metric	*Acronym*	*Mean*	*Range of variation (min–max)*
Heterozygosity (neutral)	H_{neut}	0.114	0.111–0.117
Local F_{ST} (neutral)	F_{STneut}	0.0037	0.0028–0.0071
Heterozygosity (adaptive)	H_{adapt}	0.126	0.072–0.180
Local F_{ST} (adaptive)	$F_{STadapt}$	0.074	0.059–0.097
Population adaptive index	PAI	3.75	3.05–4.89
Adaptive score	S_{adapt}	0.563	0.486–0.640

**Adaptive metrics are based on candidate markers.*

Spatial interpolation showed minimal spatial variation in H_{neut} as a consequence of low variation across sampled sites (Appendix S1). Genetic differentiation at putatively neutral SNPs was elevated in northwestern BC and low elsewhere. At candidate SNPs, H_{adapt} showed a latitudinal gradient, with values increasing northwardly, but $F_{STadapt}$ showed no clear latitudinal patterns. The adaptive score showed an inverse pattern to H_{adapt} (Appendix S1), which may reflect geographic variation in selective processes maintaining higher levels of polymorphism at candidate loci in the north than in the south. Finally, PAI showed a similar pattern to $F_{STadapt}$ (Appendix S1). Pearson's correlation tests confirmed the positive association between $F_{STadapt}$ and PAI ($r = 0.89$, $p < 0.001$) and the negative association between H_{adapt} and S_{adapt} ($r = -0.96$, $p < 0.001$); all other correlations were nonsignificant.

Alternative Genomic Metrics in SCP

Comparing across neutral genomic metrics, SCP solutions differed depending on whether H_{neut} or F_{STneut} was prioritized (Fig. 2a, b). Solutions for the 2 scenarios had low similarity (Jaccard index = 0.35) (Table 3). The solution based on H_{neut} selected priority areas in the central coast, whereas this region was excluded by the SCP scenario based on F_{STneut}.

Focusing on adaptive genomic metrics with candidate SNPs also showed that the summarizing metric affected the prioritization solution. The priority area based on H_{adapt} was primarily in the north (Fig. 2c), priority

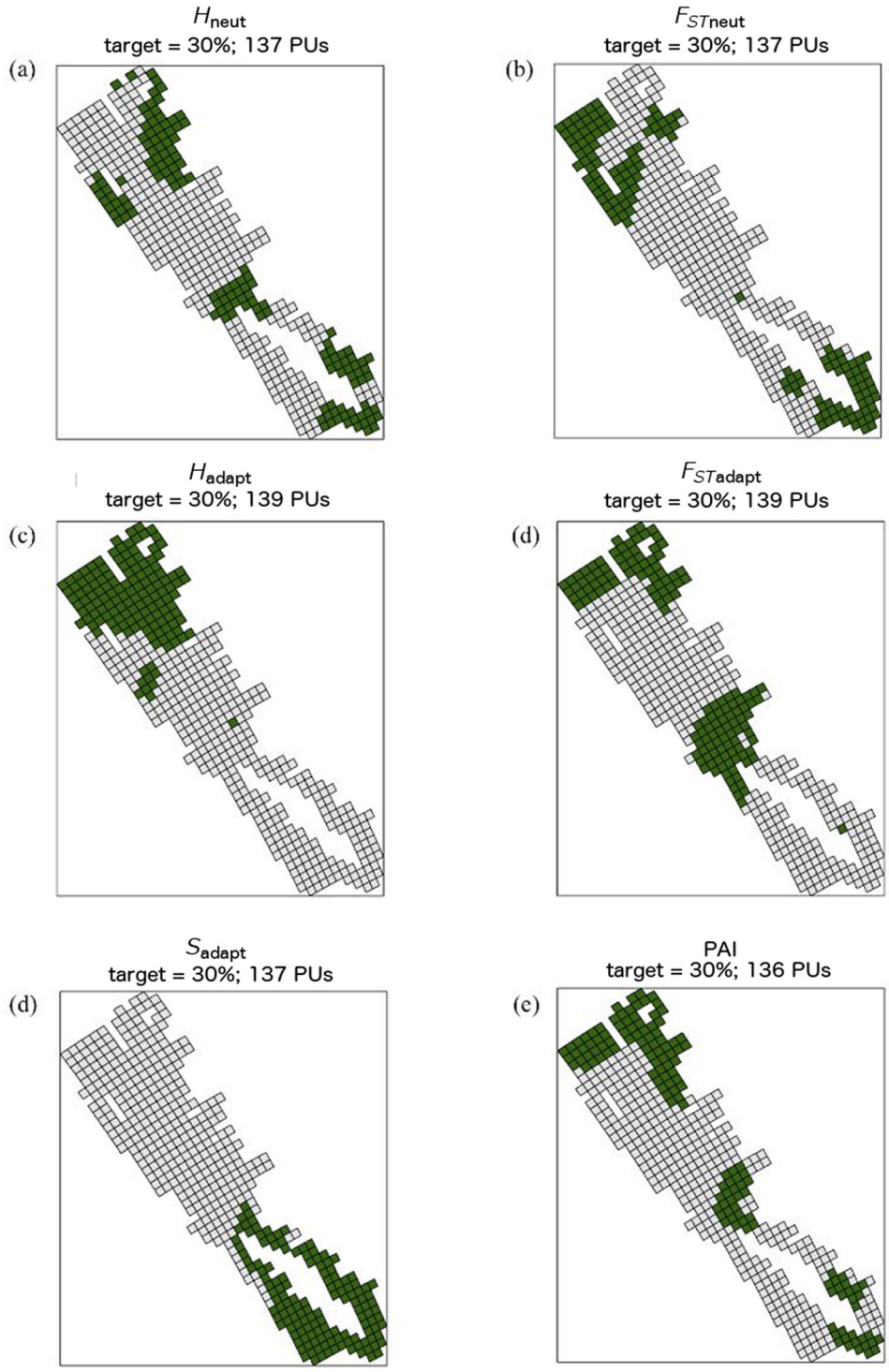

Figure 2. Alternative best solutions from prioritizr showing the selected planning units (filled grid cells) for different, individual genomic metrics based on neutral or candidate genomic markers from P. californicus *(PAI, population adaptive index; PU, planning unit).*

areas based on $F_{STadapt}$ were in the northern and central regions (Fig. 2d), and priority areas based on S_{adapt} were in the south, where there was a higher frequency of warm-temperature-associated alleles (Fig. 2e). Accordingly, solutions based on H_{adapt} and S_{adapt} independently shared no overlapping PUs (Table 3). The 2 most similar solutions (Jaccard index = 0.52) were based on metrics of adaptive distinctness ($F_{STadapt}$ and PAI). These SCP results were consistent across different subsets of candidate SNPs (Appendices S2 and S3).

Similar SCP solutions were obtained when we increased PU size (40 × 40 km) (Appendix S4). Varying the conservation targets also resulted in similar spatial outcomes with fewer (15%) or more (50%) selected PUs across the coastline (Appendices S5 and S6). In general, similarity between scenarios increased

Table 3. Jaccard coefficient of similarity between each pair of spatial conservation prioritization solutions based on single neutral or adaptive genomic metrics.

	F_{STneut}	H_{adapt}	$F_{STadapt}$	S_{adapt}	*PAI*
H_{neut}	0.350	0.211	0.216	0.274	0.429
F_{STneut}		0.243	0.160	0.274	0.319
H_{adapt}			0.318	0	0.403
$F_{STadapt}$				0.042	0.519
S_{adapt}					0.152

as protection targets increased, except in 2 comparisons (H_{neut} vs. S_{adapt} and H_{adapt} vs. PAI) in which some nonoverlapping PUs were selected with a larger protection target and the Jaccard similarity decreased slightly (Appendix S7).

Comparing Neutral and Candidate Markers in SCP

The SCP outcomes based on independent metrics differed between putatively neutral and candidate SNPs. With H_{neut}, groups of PUs throughout the region were selected, whereas the solution based on H_{adapt} selected PUs concentrated in the north (Fig. 2a, c). Jaccard similarity between these 2 solutions was low (Table 3). Likewise, outcomes based on F_{STneut} and $F_{STadapt}$ exhibited low similarity. With F_{STneut} much of the southern region was selected, whereas $F_{STadapt}$ prioritized areas concentrated in the central and northern regions.

The selection frequency of PUs across the 1000 subsets of 51 randomly selected neutral SNPs was high for PUs selected based on the full neutral data set, whereas PUs selected with the 51 candidate SNPs were rarely selected across the neutral subsets (Appendix S8) for both heterozygosity and local F_{ST}. A solution based on the top 30% of the most frequently selected PUs across resampled data sets was also similar to the solution obtained using the full neutral data set (Appendix S8). The median Jaccard similarity index comparing the solution with 51 candidate SNPs with all solutions based on resampled neutral data sets was low for both H_{neut} and F_{STneut} (0.17 and 0.13, respectively). These results imply the differences between neutral and candidate SNP data sets are not likely due to a difference in the number of markers used.

Combining Genetic Metrics

Combining H_{neut} and F_{STneut} resulted in the selection of PUs across the entire planning area (Fig. 3a), similar to the solution with H_{neut} alone (Appendix S9). However, fewer PUs in the central coast and southernmost regions were selected relative to the solution based only on H_{neut}. With a combination of H_{adapt} and $F_{STadapt}$, the solution was similar to that based only on $F_{STadapt}$ (Appendix S9) and primarily selected sites in the northern and central regions (Fig. 3b). Neither H_{adapt} nor $F_{STadapt}$ selected PUs in the southern portion of the planning area when used alone.

When H_{neut} and H_{adapt} were combined, PUs across the entire planning area were selected (Fig. 3c). This spatial pattern resembled that of H_{neut} alone; however, more PUs were selected in the north when both metrics were incorporated such that the combined solution was equally similar to both independent scenarios (Appendix S9). Combining F_{STneut} and $F_{STadapt}$ resulted in an intermediate solution. While priority areas in the central coast were largely excluded in the solution based only on F_{STneut}, and only three PUs were selected in the south with $F_{STadapt}$ alone, combining both metrics selected a large priority area in the central coast and more PUs in the south (Fig. 3d).

Combining H_{adapt} with S_{adapt}, which independently led to opposing solutions, also favored an intermediate solution; priority areas were focused in the north, south, and central coasts (Fig. 3e). Priority areas were also spread along the coast when PAI and S_{adapt} were combined (Fig. 3f). This solution was similar to that based on PAI alone but included a large area on the southwestern coast of Vancouver Island, reflecting the large priority area in this region when only S_{adapt} was considered.

Discussion

Although the value of genomic data for conservation planning has been discussed widely (Funk et al. 2012; von der Heyden 2017; Flanagan et al. 2018), the actual uptake has been stymied by a lack of clear guidelines for implementation (Shafer et al. 2015). For marine conservation, several studies have made important contributions by illustrating how neutral genetic data can be incorporated into SCP for single (Beger et al. 2014) and multispecies (Nielsen et al. 2017) objectives. Adaptive genomic markers provide complementary information regarding evolutionary resilience (von der Heyden 2017). By incorporating them into SCP, it may be possible to disentangle demographic and selective processes driving divergence. We used genomic metrics computed on putatively neutral and candidate markers identified from *P. californicus* to compare SCP solutions. Optimal priority areas varied depending on the genomic metric, type of genomic marker, and whether genomic metrics were used individually or jointly. Spatial patterns of genetic variation at neutral and adaptive loci were generated by different underlying evolutionary processes (e.g., limited connectivity or selection driving population divergence), which was reflected in the dissimilar SCP solutions obtained when using either neutral SNPs or candidate SNPs from *P. californicus* (Fig. 2). Our results have implications for decision-making regarding the treatment of genomic data in SCP and highlight the importance of

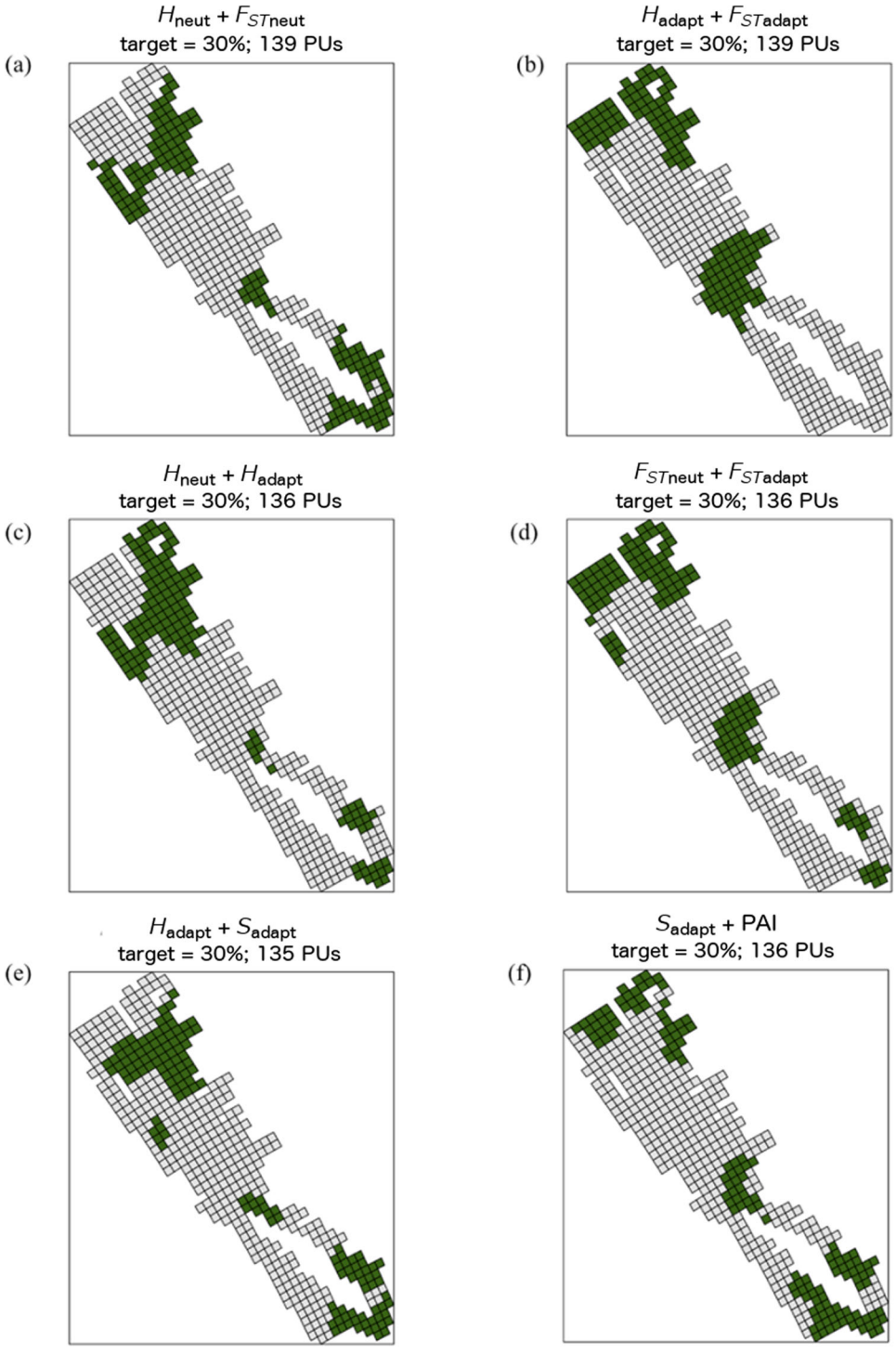

Figure 3. Alternative best solutions from prioritizr showing the selected planning units (filled grid cells) for different combinations of genomic metrics based on neutral or candidate genomic markers from P. californicus *(PAI, population adaptive index; PU, planning unit).*

carefully choosing suitable metrics to ensure they align with conservation objectives.

Choosing Genomic Metrics to Match Conservation Objectives

We found that the specific metric had a strong effect on SCP outcomes. Notably, most solutions based on a single genomic metric had very little overlap with each other (Table 3). These results support earlier findings based on neutral genetic data (Beger et al. 2014), which emphasize that the manner in which genetic data are summarized can drastically alter SCP solutions and underscore the importance of choosing metrics that adequately reflect the target genetic or genomic feature (e.g., distinctness or uniqueness, diversity, predicted "adaptedness").

One approach to conservation in rapidly changing environments is to prioritize populations predicted to persist under future conditions (Wilson et al. 2020). If

environmental change can be forecasted with confidence, then populations that have already experienced directional selective pressures may be adapted to future conditions. The adaptive score S_{adapt} is one useful metric to assign value of the potential for local adaptation in relation to well-identified selective pressures (Manel et al. 2018). For *P. californicus*, S_{adapt} was highest in PUs hosting the highest frequencies of warm-associated alleles in the southern region, and the SCP algorithm identified these PUs as priority areas when S_{adapt} was prioritized. In many cases, environmental conditions and the degree to which they will change at local versus regional scales cannot be forecasted precisely (Payne et al. 2016; Steen et al. 2017). Although there are strong ongoing trends, such as warming (Cheng et al. 2019), this level of uncertainty puts forth the question of whether a strategy aimed at "picking the winners" (Webster et al. 2017) (i.e., prioritizing sites with high S_{adapt}) is appropriate. In this case, an approach may be to "let nature choose the winners" (Webster et al. 2017) by prioritizing sites with the highest degree of adaptive genetic diversity (i.e., those with high H_{adapt}), thus preserving evolutionary potential for an uncertain future (Hoffmann et al. 2017). For *P. californicus* in BC, prioritizing H_{adapt} led to a completely nonoverlapping solution when compared with the solution based on S_{adapt}, where only northern PUs were prioritized with H_{adapt}. These conflicting solutions reflected the spatial patterns in H_{adapt} and S_{adapt}, which could be attributed to regional variation in selective processes (Véliz et al. 2004). Divergent selection may generate reduced genomic diversity in the south, while balancing selection, perhaps associated with higher temporal variance in thermal conditions, may contribute to maintaining a higher degree of polymorphism in the north (Bernatchez 2016).

Another approach for SCP with genomic metrics is to consider the distinctness or uniqueness of alleles present across protected areas (Souto et al. 2014; Nielsen et al. 2017), which can be achieved using metrics such as PAI or local F_{ST}. This is related to the objective of representativeness in SCP, whereby PUs are selected for protection such that the full variety of biodiversity is represented across selected reserve sites (Margules & Pressey 2000). Using metrics based on distinctness, either neutral or adaptive, should lead to a set of PUs with high diversity across the planning area by selecting dissimilar sites, thus preserving a wider variety of genetic diversity across protected areas, but will not necessarily prioritize individual PUs that contain the highest levels of within-PU genetic diversity. This is indeed the principle behind the development of the PAI, whereby populations are not considered for protection based on their individual levels of intrinsic diversity, but rather on their unique contribution to overall diversity relative to each other (Bonin et al. 2009). As such, it is important to clarify whether the conservation goal is to protect specific sites with the highest levels of adaptive genetic diversity (i.e., heterozygosity) or to preserve a portfolio of sites that harbor different genomic variants (e.g., PAI or F_{ST}). This difference is analogous to species-based conservation objectives related to protecting sites containing the highest levels of within-site species richness or prioritizing sites with high endemicity such that unique species are conserved across all protected sites.

Combining Multiple Genomic Metrics in SCP

Combining genomic metrics within a single SCP scenario may be a useful way to protect multiple evolutionary processes. For example, combining H_{adapt} and S_{adapt}, which independently led to opposing solutions, selected some PUs that contained a high frequency of alleles associated with warm temperatures, which are likely to be beneficial under future warming, and selected other PUs that harbor high levels of polymorphism. This combination also yielded a more spatially representative solution than either independent metric, which is likely to be favorable for preserving genetic diversity across the whole coast for *P. californicus*, especially when connectivity is somewhat restricted between the north and south (Xuereb et al. 2018*a*).

The SCP solutions differed substantially when we used either candidate adaptive markers or putatively neutral markers (Fig. 2). This implies that neutral genomic markers are not effective surrogates for adaptive genetic variation in this system and that candidate adaptive genomic markers provide different information compared with putatively neutral markers. In particular, although neutral genetic markers provide information on demographic history, population structure and connectivity, adaptive markers inform on local adaptation to environmental conditions and the type of selection (e.g., divergent vs. balancing) at play. Combining metrics based on putatively neutral and adaptive genomic markers may thus be a useful strategy for capturing spatial patterns of population genetic variation generated by different processes, such as demographically independent and adaptively differentiated populations, at the same time (Funk et al. 2012).

Perspectives on Using Genomic Data in SCP

Although the integration of genomic data in SCP holds great promise, several challenges and decisions pertaining to the treatment of these data arise. First, the identification of candidate adaptive loci relies on statistical tests that are prone to errors (de Villemereuil et al. 2014) may only capture a moment in time (Villacorta-Rath et al. 2018), and sometimes result in different sets of candidate loci (e.g., Dalongeville et al. 2018). For nonmodel organisms, annotated reference genomes and transcriptomes are often lacking and experimental validation may

be unfeasible; thus, linking candidate adaptive markers to gene functions and adaptive traits remains a challenge. However, we found that SCP solutions were very similar between candidate adaptive SNPs detected by two different methods (RDA and BayeScan), suggesting that, at least for *P. californicus*, SCP is not affected by the detection method of candidate loci. Future studies should focus on the robustness of SCP solutions to errors in the detection of candidate adaptive loci and the variability introduced in the solutions relative to other sources of uncertainties.

Second, in real planning efforts, solutions will ideally be based on candidate genomic markers associated with multiple environmental variables. To illustrate the decision-making involved in using genomic data in SCP, we focused exclusively on associations with mean bottom temperature, which is a key variable for marine ectotherms (Bay & Palumbi 2014; Benestan et al. 2016). However, other environmental variables, such as salinity and pH, may also play important roles in driving patterns of adaptive genetic variation in *P. californicus* (e.g., Xuereb et al. 2018*b*) and other marine species (Dalongeville et al. 2018; Griffiths et al. 2019). Moreover, global change is expected to lead to greater temporal fluctuations in temperature over shorter time scales (Sommer et al. 2018). In such a case, SNPs associated with temperature variability, in addition to average temperature, should also be considered in the future. Results of other studies suggest that environmental data could be used as a surrogate for adaptive genomic data (Hanson et al. 2017). Additional studies in this region should explore the extent to which SCP solutions based on environmental data capture adaptive genomic patterns. Finally, although we focused on environmental sources of selection pressures in this study, other factors, including fishing pressures, may also influence adaptation (Fenberg & Roy 2008). Research into the potential adaptive consequences of fishing-induced evolution in *P. californicus* populations is thus warranted.

Third, SCP is usually performed in a multispecies multiobjective framework with a suite of physical, biological, and socioeconomic variables. While recent studies have evaluated the use of neutral genetic metrics for multispecies SCP objectives (Nielsen et al. 2017; Paz-Vinas et al. 2018), future work should also focus on understanding how adaptive variation may vary between species (e.g., Stanley et al. 2018) and thus could influence SCP outcomes. It will be important to consider how these genomic-based features should be weighed in light of multiple objectives and in conjunction with other variables including abundance or biomass, catch rates for harvested species, and other costs associated with individual PUs. The inshore waters of BC support a variety of economic activities (fishing, aquaculture, marine tourism, transportation, and mining) and the governments of Canada, British Columbia, and First Nations have taken action to create a network of MPAs through systematic conservation planning (MPA Network 2020). Given the ongoing SCP work in coastal BC, as genomic data become available for diverse taxa, they will add an important element to the prioritization process. While the specific metrics used to summarize genomic data will ultimately depend on the conservation objectives, evaluating spatial patterns of putatively neutral and adaptive genomic variation provides valuable information regarding different ecological and evolutionary processes that can be incorporated directly into conservation planning to promote long-term biodiversity persistence.

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Supporting Information

Spatial interpolation of metrics (Appendix S1), alternative SCP solutions for different subsets of candidate SNPS (Appendices S2.S5), SCP solutions with alternative planning unit size (Appendix S6) and conservation target (Appendices S7.S8), results based on resampling of the neutral dataset (Appendix S9), and jaccard similarity between SCP solutions based on combined genomic metrics (Appendix S10) 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.

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