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PRIMARY RESEARCH ARTICLE

Genomic vulnerability of a dominant seaweed points to future-proofing pathways for Australia's underwater forests

Georgina Wood[1,2] | Ezequiel M. Marzinelli[1,3,4] | Alexandra H. Campbell[5] | Peter D. Steinberg[2,3,4] | Adriana Vergés[2] | Melinda A. Coleman[6]

[1]School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

[2]Centre for Marine Science and Innovation, School of Biological, Earth and Environmental Sciences, UNSW Sydney, Sydney, NSW, Australia

[3]Sydney Institute of Marine Science, Sydney, NSW, Australia

[4]Singapore Centre for Environmental Life Sciences Engineering, Nanyang Technological University, Singapore, Singapore

[5]USC Seaweed Research Group, University of the Sunshine Coast, Sunshine Coast, Qld, Australia

[6]Department of Primary Industries, National Marine Science Centre, Coffs Harbour, NSW, Australia

Correspondence
Georgina Wood, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
Email: georgina.wood@sydney.edu.au

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Abstract

Globally, critical habitats are in decline, threatening ecological, economic and social values and prompting calls for 'future proofing' efforts that enhance resilience to climate change. Such efforts rely on predicting how neutral and adaptive genomic patterns across a species' distribution will change under future climate scenarios, but data is scant for most species of conservation concern. Here, we use seascape genomics to characterise genetic diversity, structure and gene-environmental associations in a dominant forest-forming seaweed, *Phyllospora comosa*, along its entire latitudinal (12° latitude), and thermal (~14°C) range. *Phyllospora* showed high connectivity throughout its central range, with evidence of genetic structure and potential selection associated with sea surface temperatures (SSTs) at its rear and leading edges. Rear and leading-edge populations harboured only half the genetic diversity of central populations. By modelling genetic turnover as a function of SST, we assessed the genomic vulnerability across *Phyllospora's* distributional range under climate change scenarios. Despite low diversity, range-edge populations were predicted to harbour beneficial adaptations to marginal conditions and overall adaptability of the species may be compromised by their loss. Assisted gene flow from range edge populations may be required to enhance adaptation and increase resilience of central and leading-edge populations under warming oceans. Understanding genomic vulnerability can inform proactive restoration and future-proofing strategies for underwater forests and ensure their persistence in changing oceans.

KEYWORDS
assisted evolution, future-proofing, GDM, genetic diversity, kelp, marine ecology, restoration, seascape genomics, seaweed, SNP

1 | INTRODUCTION

Current rates of environmental and climate change are outpacing the ability of species to adapt and evolve (Burrows et al., 2011; Cang et al., 2016; Deutsch et al., 2015; Radchuk et al., 2019) resulting in global range shifts and species losses (Chen et al., 2011; Poloczanska et al., 2013). It is clear that relying only on preserving or even restoring ecosystems to historic or current states is unlikely to be effective under future climates (Breed et al., 2018; Martínez et al., 2018; Perring et al., 2015), prompting calls for proactive interventions that anticipate and prepare for change (Coleman, Wood, et al., 2020; Rossetto et al., 2019; van Oppen et al., 2015). One type of intervention which is rapidly gaining interest is 'assisted evolution', which consists of

strategies to increase the resilience of wild organisms in the face of likely future environmental stress (Aitken & Whitlock, 2013; Anthony et al., 2017; van Oppen et al., 2015). These strategies include: genetic rescue, which is the introduction of individuals from genetically diverse populations in similar environments into genetically depauperate populations to enhance diversity, fitness and adaptive potential (e.g. Reynolds et al., 2012; Whiteley et al., 2015); assisted gene flow, which is the intentional movement of pre-adapted individuals within a species range to facilitate adaptation to anticipated future conditions (Aitken & Whitlock, 2013); and assisted colonisation, which is the movement of individuals of a species to suitable environments outside their native range to facilitate species' persistence (Weeks et al., 2011). Such strategies are being developed to accelerate the rate of naturally occurring evolutionary processes and boost resilience to future change.

The design of assisted evolution strategies relies on understanding underlying patterns of neutral and adaptive (ecologically relevant) genetic diversity and gene flow across a species distribution and predicting how such variation may change under future environmental conditions (Ralls et al., 2020). However, such genomic data are limited for most species of conservation concern (e.g. Bay et al., 2018; Coleman, Wood, et al., 2020), constraining our understanding of species' adaptability and vulnerability and designing pathways for intervention. Underwater seaweed forests underpin temperate coastal ecosystems on rocky shores and hold significant ecological and economic value (Bennett et al., 2016; Coleman & Wernberg, 2017), but are in decline in many places around the world (Krumhansl et al., 2016; Wernberg et al., 2019). While causes of decline vary, temperature stress associated with ocean warming and marine heatwaves is among the most pervasive causes of loss (Smale, 2020; Wernberg et al., 2011, 2016). Heat stress can directly affect seaweed survival, condition and resilience to additional perturbations (Wernberg et al., 2010) and can also make seaweeds more vulnerable to consumers (Provost et al., 2017; Simonson et al., 2015; Vergés et al., 2014) and disease (Qiu et al., 2019). Mortality associated with temperature stress can also lead to decreases in genetic diversity and adaptive capacity (Coleman, Minne, et al., 2020; Coleman & Wernberg, 2020; Gurgel et al., 2020).

South-eastern Australia harbours the highest number of endemic seaweeds in the world (Bennett et al., 2016; Phillips, 2001), but it is warming three times faster than the global average (Hobday & Pecl, 2014; Ridgeway, 2007). Under best-case carbon emission reduction scenarios, ocean warming alone is predicted to decrease the distribution of over 85% of the dominant forest-forming species in south-east Australia by 75%, by 2100 (Martínez et al., 2018). These predictions are based on single species-wide thermal tolerance data; however, losses could be even more widespread if intraspecific variation in thermal tolerance exists (Miller et al., 2020) or if range shifting herbivores accelerate declines (Vergés et al., 2016). Conversely, variation in thermal tolerance could also naturally or artificially mitigate losses. With such a high risk of losing key habitat-forming species and the major ecological changes that would consequently occur along this coastline, Australian seaweed forests are excellent candidates for assisted evolution (Wood et al., 2019). However, such efforts are hampered by a lack of knowledge of macroalgal functional genomics and adaptive potential that underpin such strategies (Coleman & Wernberg, 2020; Coleman, Wood, et al., 2020).

Phyllospora comosa (hereafter *Phyllospora*) is an endemic, monotypic, forest-forming seaweed inhabiting the south-eastern Australian coastline that supports vital ecosystem functions, unique biodiversity and economic values (Bishop et al., 2010; Coleman & Wernberg, 2017; Marzinelli et al., 2014). *Phyllospora* has suffered historical declines in Sydney—the middle of its range, likely due to poor water quality (Coleman et al., 2008), and is the subject of Australia's largest macroalgal restoration programme (see www.operationcrayweed.com; Campbell et al., 2014; Layton et al., 2018; Vergés et al., 2016). However, *Phyllospora* is particularly vulnerable to ocean warming and heatwaves (Straub, 2019), and its long-term persistence in extant and restored areas is significantly threatened by climate change, with a projected 87% loss in distribution by 2100 (Martínez et al., 2018). Assisted evolution strategies may play a critical role in boosting the resilience of this key species and facilitating its survival into the future.

Here, we developed a genomic toolbox to inform future-proofing strategies for *Phyllospora*. We characterised neutral and adaptive genetic diversity and structure across the species' entire latitudinal

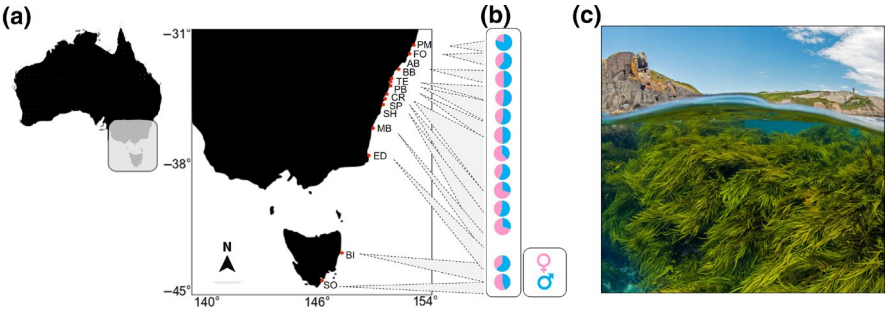


FIGURE 1 Field sampling of *Phyllospora comosa* at sites in Australia. (a) Map with inset depicts the latitudinal and longitudinal extent of *Phyllospora*'s distributional range. PM, Port Macquarie; FO, Forster; AB, Anna Bay; BB, Bateau Bay; TE, Terrigal; PB, Palm Beach; CR, Cronulla; SP, Shark Park; SH, Shellharbour; MB, Malua Bay; ED, Eden; BI, Bicheno; SO, Southport. (b) Sex ratios of sampled individuals at each site (pink = female, blue = male) and (c) photograph of typical *Phyllospora* reef habitat

(31–43°) and thermal (~12–26°C) range. We then used these data to model genetic composition as a function of temperature variables and predict future genomic vulnerability to inform proactive management and conservation strategies.

2 | METHODS

2.1 | Field sampling

We sampled 13 sites spread across *Phyllospora's* latitudinal range over the Austral summers of 2016 and 2018 (five sites in 2016, seven sites in 2018 and one site in both years; Figure 1). *Phyllospora* occurs in shallow coastal waters only within this range (0–6 m depth on mainland Australia, 0–18 m depth in Tasmania). None of the sampled sites had been previously restored; however, we note that there had been two small-scale reciprocal transplantations of 20 algae (40 individuals in total) between Palm Beach and Cronulla during previous experiments (Campbell et al., 2014), none remaining at the time of sampling. Given the genetic similarity of these sites with other sites nearby (see Section 3), we do not believe that these small-scale transplants have influenced the genetic signature of *Phyllospora* at these sites. At each site, a minimum of 20 and maximum of 50 (in accordance with current advice on sampling for high-throughput sequencing methods; see Mao et al., 2020; Morin et al., 2009; Nazareno et al., 2017; Rhode et al., 2017) reproductive *Phyllospora* individuals (whole male and female thalli; >1 m apart) were haphazardly sampled from a 500-m^2 area of reef at <6 m depth. To assess any biases in sex ratios at each site, the sex of each individual was recorded via visual inspection of receptacles, as these differ in shape among males and females (Burridge et al., 1993). Ratios were mostly equal, with the exception of the northern-most site, Port Macquarie, where there were >50% more males than females (Figure 1). Ten unfouled apical tips were removed from each individual for genotyping. Samples were rinsed in fresh water and dried to remove external salt, epiphytes and water (see Coleman & Brawley, 2005), then snap-frozen in liquid nitrogen and stored at −80°C. DNA extraction and genotyping was done as per Wood et al. (2020).

One hundred and fifty-six samples from across the eight sites were genotyped using an Agena Bioscience MassARRAY with iPlex GOLD technology on a custom panel of 354 single nucleotide polymorphism (SNP) loci. These had been previously established by genotyping by sequencing runs of seven samples at the Australian Genome Research Facility (www.agrf.org.au) that were subjected to preliminary assay design (MassARRAY software) to select the top SNPs with a high minor allele frequency (MAF) and reasonable flanking sequence.

2.2 | Bioinformatics

Bioinformatics and data analyses were conducted using the statistical platform R (version 3.6; R Core Team, 2019). Because they are based on thresholds calculated across populations, quality filtering steps may erroneously remove private alleles, that is those found in high frequencies at differentiated populations. We thus first checked for private alleles in the raw data using the R package *poppr*. As private alleles were found in low frequencies (see Table 1), any subsequent removal due to filtering steps was deemed unlikely to affect overall results. We then quality filtered the data, excluding SNPs and samples with a call rate (i.e. rate of non-missing data) below 90% of the total, or with a MAF below 0.05. We also filtered for linkage disequilibrium (non-random association/correlation of alleles) using *SNPrelate* (Zheng et al., 2012) with a threshold value of

TABLE 1 Genetic diversity of *Phyllospora comosa* populations across its latitudinal range, ordered from north to south, based on 109 loci

Site	*n*	PA[a]	F_{IS}[b]	H_O	H_E	AR
Port Macquarie	20	2	0.116	0.175	0.184	1.752
Forster	20	0	**−0.051**	0.206	0.197	1.587
Anna Bay	20	2	0.064	0.256	0.273	1.841
Bateau Bay	26	0	−0.004	0.332	0.331	1.929
Terrigal	29	1	0.009	0.338	0.340	1.945
Palm Beach	29	0	0.012	0.310	0.317	1.947
Cronulla	49	1	−0.021	0.335	0.327	1.957
Shark Park	29	4	**−0.042**	0.319	0.304	1.896
Shellharbour	30	1	0.001	0.309	0.304	1.894
Malua Bay	20	1	0.002	0.336	0.336	1.919
Eden	20	0	**−0.036**	0.312	0.296	1.825
Bicheno	20	0	−0.016	0.234	0.231	1.711
Southport	19	0	−0.035	0.179	0.172	1.523

Abbreviations: AR, rarefied allelic richness; H_E, expected heterozygosity; H_O, observed heterozygosity.

[a]Private alleles (total number).

[b]Inbreeding coefficient (F_{IS}). Values that differ significantly from zero are shown in bold.

0.7, which removed two loci from the dataset. Exact tests for Hardy–Weinberg equilibrium (HWE) deviations were calculated across all samples and loci in the dataset using *hierfstat* (Goudet, 2005) and corrected for multiple testing using the Benjamini–Hochberg false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995). 45% of loci deviated from the HWE, but only at one or two sites, so these loci were retained in the dataset. One locus was identified as deviating from HWE at 10 (77%) sites and exhibited high heterozygote deficiencies (FIS = 0.918). We removed this locus as this is likely due to null alleles or other genotyping errors (Hosking et al., 2004). An initial comparison of observed heterozygosity and sample size for each site established that the use of unbalanced samples did not bias genetic diversity estimates (Table 1), so all samples were included for subsequent analysis. This left a total of 109 out of the original 354 loci across 331 of the original 337 samples.

2.3 | Data analyses

2.3.1 | Population genetic diversity and structure

Genetic differentiation and diversity of *Phyllospora* at each site were first evaluated by generating estimates of observed heterozygosity (H_O) and expected heterozygosity (H_E) for each locus and for each sampling group using the *diveRsity* package (Keenan et al., 2013), and allelic richness (AR) with allele counts rarefied by the minimum number of individuals genotyped using *hierfstat*. We tested for differences in expected heterozygosity between sites using the *Hs.test* function in *adegenet*. We also calculated departures from random mating ($F_{IS,}$ i.e. inbreeding/outbreeding estimates) for the overall dataset and assessed significance using 1000 permutations with 95% confidence intervals.

Genetic structure of the sampled populations was then visualised using principal component analysis (PCA) and statistically assessed using two approaches: Wier and Cockham's F_{ST} (the proportion of genetic variance contained in a subpopulation relative to the total genetic variance) and *sNMF* (Frichot et al., 2014). Pairwise comparisons of linearised F_{ST} between sampling locations and their significance was assessed using *p*-values calculated via bootstrapping (999) in the *dartR* package (Gruber et al., 2018) and corrected using the Benjamini–Hochberg FDR procedure. *sNMF* is based on sparse non-negative matrix factorisation to estimate the genetic ancestry components for each individual. Fifteen runs were performed with $\alpha = 10$ for each *K* value (1–14). Cross-entropy was used to guide the choice of the number of ancestral populations and the results from the best run were visualised using the barplots function.

2.3.2 | Scaling from genetic data to seascape-level predictions

To examine the potential role of climatic factors in driving *Phyllospora's* genetic structure, we used distance-based linear models and redundancy analysis (dbRDA; McArdle & Anderson, 2001) in the *vegan* package (Oksanen et al., 2018) and generalised dissimilarity modelling (GDM) in the *gdm* package (Manion et al., 2017). We then used the GDM model to predict the distribution of *Phyllospora* genetic variation across the seascape under current environmental conditions and how that may change under predicted future climates.

We first screened for important environmental predictors by fitting the overall genetic data (major SNP allele frequency scored for each individual) to several variables based on sea surface temperature (SST) using dbRDA. Missing allele frequencies were imputed using *sNMF* in the *LEA* package (Frichot & François, 2015) using the most common allele frequency observed in each genetic cluster ($K = 12$; see Section 3.2). SST data for present (2000–2014) environmental conditions based on monthly averages were downloaded from the Bio-ORACLE marine layer database (Assis et al., 2017; Tyberghein et al., 2012) and input into R using the *raster* package (Hijmans, 2017). We calculated annual maximum, minimum, range, variation (standard deviation) and mean using the monthly data. Environmental variables that were strongly correlated (Pearson's $r^2 > 0.6$) were removed, leaving one in the set to represent those removed. The final model included the average of annual maximum and range in SST occurring at each site.

Turnover of genetic (neutral and adaptive) variation as a function of SST variables was then assessed using generalised dissimilarity models (GDMs), which analyse and map patterns of turnover in genetic composition using nonlinear functions of environmental gradients. We fitted the GDM model using the linearised pairwise population F_{st} outputs from DartR and assessed the output plots using the maximum height of each curve, which indicates the total amount of turnover in allele frequencies associated with that variable, and by extension, the relative importance of that variable in explaining changes in allele frequency, holding all other variables constant. The shape of each function indicated how the rate of change in allele frequencies varies along the gradient. We then transformed the SST max and SST range rasters based on the model splines (*gdm.transform*) and predicted across space (*predict*), using a raster mask which defined the spatial extent using the latitudinal limits of *Phyllospora's* distribution (Fitzpatrick & Keller, 2015).

We also projected the model onto a predicted future environmental landscape with the same procedure, except we replaced the current bioclimatic rasters with the future ones for 2100 that were predicted under a low (RCP 26) and high (RCP 85) CO_2 emission scenario (extracted from the Bio-ORACLE database). We calculated 'genomic vulnerability' (Bay et al., 2018), which is the amount genomic change (as F_{ST}) required to track environmental change over time, using the *predict* function with time = TRUE.

2.3.3 | Detecting climate-related candidate SNP loci

We identified loci which are associated with SST and thus may represent patterns of adaptation using two approaches to increase

robustness of results (Benestan et al., 2016; Rellstab et al., 2015). We first identified SNPs that show (i) strong associations between allele frequencies and environmental gradients (Frichot et al., 2013) and (ii) extreme allele frequency divergence among populations (F_{ST}; Foll & Gagliotti, 2008).

For (i) we used latent factor mixed models (LFMM; Frichot et al., 2013), which detects outlier loci associated with environmental variables whilst accounting for the confounding effects of population structure. Missing allele frequencies were imputed using *sNMF* (Frichot et al., 2014) in the *LEA* package (Frichot & François, 2015) using the most common allele frequency observed in each genetic cluster (K = 12; see Section 3.2). Outlier loci associated with SST variables that had been identified as important with dbRDA were then identified using *z*-score cut-off in the *lfmm* v2.0 package (Caye et al., 2019). The number of genetic clusters (K = 12) was fitted as a latent variable in the model. Because there were a high number of loci that were identified as significantly associated with each factor, and methods for detecting loci under selection are known to create false positives, a strict FDR correction of 0.001 was applied to determine significance. We compiled a set of 'key' outlier loci which overlapped with both variables, as a combination of these is likely important when choosing donors for assisted evolution strategies.

For (ii) we used *BayeScan* 2.1 (Foll, 2012a, 2012b; Foll & Gaggiotti, 2008), which uses a Bayesian approach to detect F_{ST} outlier loci by using linear regression to decompose F_{ST} coefficients into population- and locus-specific components and estimates the posterior probability of a locus showing deviation from Hardy–Weinberg proportions. We used prior odds of 10, which is recommended for identification of candidate loci within a few hundreds of markers (Foll, 2012) and a total of 10 separate runs, from 50,000 to 500,000 iterations with a 10% burn-in period. An FDR correction of 0.05 was applied to avoid the occurrence of false positives.

3 | RESULTS

3.1 | Genetic diversity

Genetic diversity of *Phyllospora* was relatively low overall, with observed heterozygosity (H_O) among the sites ranging from 0.172 to 0.336 and AR from 1.523 to 1.957, which demonstrated a clear trend for lower genetic diversity at sites near the rear and leading edges compared to *Phyllospora's* central range (Table 1). Pairwise tests confirmed that expected heterozygosity differed significantly between most sites and was generally more similar among sites in the central range (i.e. BB, TE, PB, CR, SP, SH and MB) and among range-edge sites (PM, FO and SO; Table 2). Most sites were characterised by small non-significant F_{IS} estimates; however, three sites (Forster, Shark Park and Eden) had significantly large, negative values indicative of outbreeding (Table 1). Importantly, almost a quarter of the loci (24%) deviated from HWE at the warm rear-edge population (Port Macquarie), suggesting non-random mating or a small effective population size in this marginal population.

3.2 | Population structure

Principal component analysis ordinations showed that sites clustered in a broad, hierarchical latitudinal pattern (Figure 2a). Pairwise F_{ST} tests using the overall SNP dataset between all pairs of sites confirmed that all sites were genetically different (all pairwise tests

TABLE 2 Test statistics[a] for pairwise comparisons of expected heterozygosity estimates between sites. Values are the difference in H_E between sites

Site	PM	FO	AB	BB	TE	PB	CR	SP	SH	MB	ED	BI	SO
PM													
FO	−0.013												
AB	**−0.089**	**−0.076**											
BB	**−0.146**	**−0.134**	**−0.057**										
TE	**−0.156**	**−0.143**	**−0.067**	−0.009									
PB	**−0.133**	**−0.12**	**−0.044**	**0.014**	**0.023**								
CR	**−0.143**	**−0.13**	**−0.054**	0.003	0.013	−0.010							
SP	**−0.119**	**−0.107**	**−0.031**	**0.027**	**0.037**	0.013	**0.024**						
SH	**−0.119**	**−0.107**	**−0.031**	**0.027**	**0.036**	0.012	**0.024**	0.000					
MB	**−0.152**	**−0.139**	**−0.063**	−0.006	0.004	−0.019	−0.009	**−0.033**	**−0.032**				
ED	**−0.112**	**−0.099**	**−0.024**	**0.034**	**0.044**	**0.042**	0.03	0.007	0.007	**0.0399**			
BI	**−0.047**	**−0.034**	**0.042**	**0.099**	**0.109**	**0.086**	**0.096**	**0.072**	**0.072**	**0.105**	**0.065**		
SO	0.012	**0.025**	**0.100**	**0.158**	**0.168**	**0.145**	**0.155**	**0.131**	**0.131**	**0.164**	**0.124**	**0.059**	

Abbreviations: AB, Anna Bay; BB, Bateau Bay; BI, Bicheno; CR, Cronulla; ED, Eden; FO, Forster; MB, Malua Bay; PB, Palm Beach; PM, Port Macquarie; SH, Shellharbour; SO, Southport; SP, Shark Park; TE, Terrigal.

[a]Significant values following false discovery rate correction are in bold.

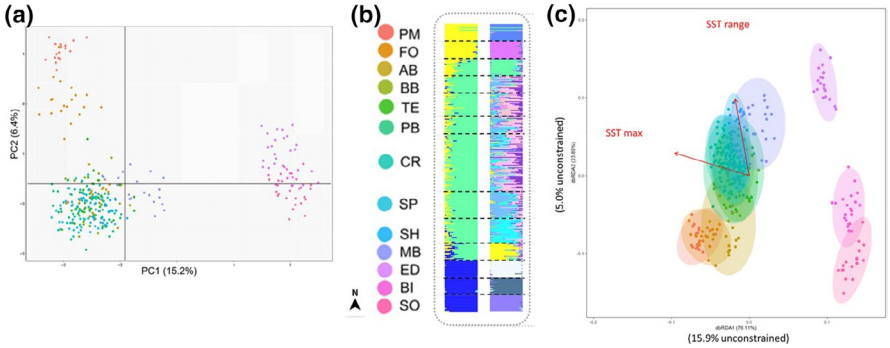


FIGURE 2 Genetic structure among sample locations. (a) Unconstrained ordination plot based on PCA. (b) Genetic structure plots showing individuals assigned to inferred clusters of K = 3 or 12 using LEA and (c) constrained ordination biplot from dbRDA model for *Phyllospora comosa* populations sampled across the latitudinal range. For (a) and (c), samples are coloured by sites. For (b), sites are organised north–south with each row of the structure plot represent an individual and different colours within columns indicate maximum likelihood probability of belonging to different genetic clusters (sites delineated with black dotted lines). Length and direction of the arrow vectors in (c) indicate strength and direction of the influence of SST max and range. dbRDA, distance-based linear models and redundancy analysis; PCA, principal component analysis; AB, Anna Bay; BB, Bateau Bay; BI, Bicheno; CR, Cronulla; ED, Eden; FO, Forster; MB, Malua Bay; PB, Palm Beach; PM, Port Macquarie; SH, Shellharbour; SP, Shark Park; SO, Southport; TE, Terrigal

TABLE 3 Population structure (pairwise F_{st}) among *Phyllospora comosa* populations based on 109 loci[a]

Site	PM	FO	AB	BB	TE	PB	CR	SP	SH	MB	ED	BI	SO
PM													
FO	0.278												
AB	0.275	0.288											
BB	0.252	0.192	0.115										
TE	0.245	0.202	0.132	0.022									
PB	0.249	0.212	0.124	0.024	0.051								
CR	0.235	0.194	0.120	0.029	0.044	0.022							
SP	0.260	0.217	0.146	0.037	0.057	0.035	0.039						
SH	0.276	0.251	0.174	0.081	0.098	0.060	0.070	0.069					
MB	0.299	0.281	0.192	0.116	0.119	0.126	0.119	0.133	0.142				
ED	0.472	0.462	0.391	0.326	0.326	0.344	0.339	0.355	0.341	0.266			
BI	0.516	0.491	0.389	0.338	0.327	0.336	0.340	0.362	0.353	0.302	0.303		
SO	0.568	0.543	0.430	0.355	0.344	0.355	0.366	0.388	0.385	0.367	0.367	0.255	

Abbreviations: AB, Anna Bay; BB, Bateau Bay; BI, Bicheno; CR, Cronulla; ED, Eden; FO, Forster; MB, Malua Bay; PB, Palm Beach; PM, Port Macquarie; SH, Shellharbour; SO, Southport; SP, Shark Park; TE, Terrigal.

[a]All pairwise values significant.

significant; Table 3) and were highly differentiated overall (global F_{ST} = 0.225). Using *LEA*, we identified the most likely number of genetic clusters in the overall dataset as 12 or 3 (Figure 2b).

3.3 | Links to seascape variables

In the dbRDA, average annual maximum SST and SST range explained a significant proportion of overall genetic differentiation in *Phyllospora* ($F_{2,328}$ = 34.16, adj-R^2 = 0.167, p < 0.001; Figure 2c). The GDM model with these two variables plus geographical distance explained 88% of the overall genetic differentiation (F_{ST}) between sampling sites. The GDM model showed a positive non-linear relationship between environmental distance and genomic distance (Figure 3a). Visual examination of the genomic distances predicted from the model versus the observed values indicated the model had reasonable predictive power (Figure 3a). Geographical distance showed a positive, non-linear relationship with genomic distance. The geographical spline predicted greatest genomic differentiation from 0 to <200 km, at which point an increase in geographical distance did not affect genomic distance until further than 800 km (Figure 3a). SST range had a similar influence on genomic distance as geographical distance, with ranges <6–7.5°C having relatively positive linear influence and sharply increasing when temperature ranges increased over 8°C. SST annual maximum showed the strongest relationship with genomic distance, with a positive, relatively

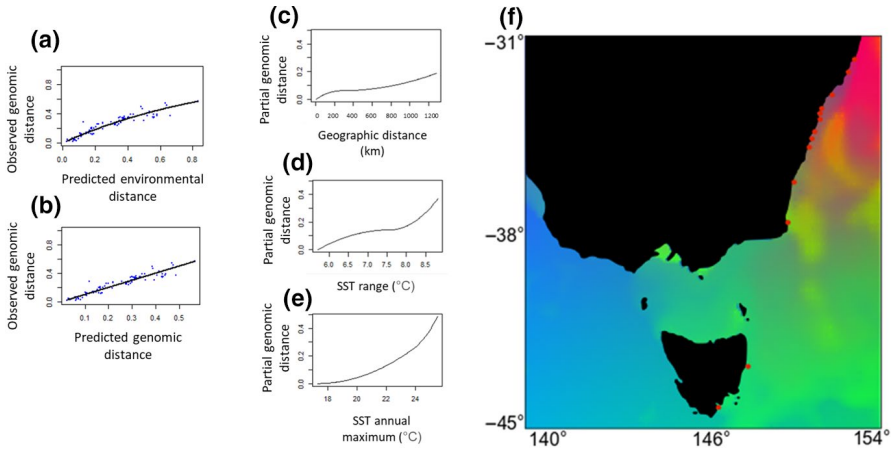
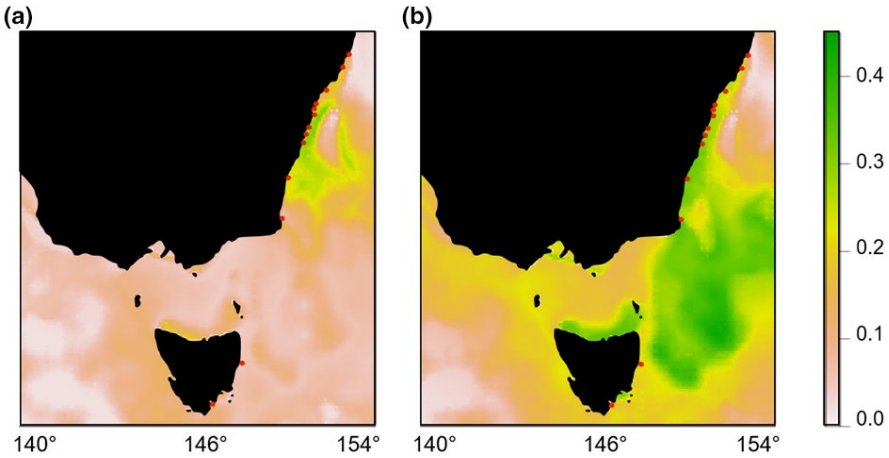


FIGURE 3 Species-wide genetic turnover plots, based on generalised dissimilarity models. (a) Non-linear relationship between predicted environmental distance and observed genomic distance. Points are site pairs; the line is the predicted relationship. (b) Relationship between predicted genomic distance and observed genomic distance. Points are site pairs; the line indicates where observation and prediction match. Model-fitted I-splines for the final model, showing predicted genomic distance/change against (c) geographical distance, (d) range in sea surface temperature (SST) and (e) maximum SST at each site. (f) Predicted spatial variation in population-level genetic composition. Colours represent gradients in genetic turnover derived from transformed environmental predictors. Locations with similar colours are expected to harbour populations with similar genetic composition. *Phyllospora comosa*'s entire potential range is shown; however, note that the species occurs only in coastal areas <18 m depth; red dots indicate sampled populations

FIGURE 4 Predicted genetic offset needed under climate change. GDM predictions based on currently modelled (a) RCP 26 and (b) RCP 85 scenarios for 2100. Map units are in F_{ST}. *Phyllospora*'s entire potential range is shown; however, note that the species occurs only in coastal areas <18 m depth; red dots indicate sampled populations. GDM, generalised dissimilarity modelling



linear relationship with genomic distance until temperatures reach >24°C. The resulting map partitioned the seascape into a number of regions with different predicted genomic compositions, including the northern-most site Port Macquarie, the central range along the NSW coast, sites around the Bass Strait and along the eastern coast of the Great Australian Bight.

3.4 | Predictions under future climates

Comparisons of the GDM model projected onto current conditions to the GDM model projected onto 2100 climate predictions under RCP 2.6 and RCP 8.5 revealed high amounts of genomic change are potentially required to keep pace with climate change along the majority of the NSW coast. Even under optimistic carbon emission scenarios, *Phyllospora* was predicted to need selection/high genetic turnover across the entirety of its range, with the need for selection or genetic turnover highest (FST of ~0.2) in the centre of NSW (Figure 4a). Under RCP 8.5, populations along the eastern coast of mainland Australia and the north region of Tasmania were predicted to need intense natural selection in order to respond to predicted ocean warming (F_{ST}~0.4).

3.5 | Signals of selection and adaptive genetic structure

We detected 83 outlier loci in total (43%); however, only one of these was identified through both LFMM and *BayeScan* (Table S1). LFMM identified 58 loci that were associated with maximum SST and 52 loci that were associated with the range in SST. Overall, there were 28 loci that had overlapping associations with both of these temperature variables. In the *BayeScan* program, we detected two polymorphic loci with statistically significant patterns

of divergent genetic differentiation, one of which was also identified using LFMM (Figure 5a).

Using LEA, we determined the optimum number of genetic clusters for outlier SNPs associated with both SST max and range as $K = 4$ (Figure 5b). Visual assessment of the results with a barplot revealed significant structure between the northern-most sites (Port Macquarie, Forster and Anna Bay) and central sites (Figure 1b), which typically vary in temperature by just 0.5–3°C. Patterns of allele frequencies at the SNP loci identified by all outlier methods exhibited little differentiation between sites from the northern range edge and central range, however, with greatest differentiation between these and the southern-most mainland (Eden) and Tasmanian sites, which typically differ in temperature by 3–6°C (Figure 5c).

4 | DISCUSSION

There is an urgent need for interventionist approaches such as assisted evolution that enhance ecosystem resilience to environmental changes. However, the genetic information needed to sensibly implement such interventions is critically lacking for most species. Our study characterised genetic structure and diversity of the declining forest-forming seaweed *Phyllospora* and how it related to SST across its latitudinal and thermal range. *Phyllospora* had relatively high gene flow, indicating high connectivity over generations at regional scales; however, genetic diversity was generally greatly reduced at the range edges. While low diversity at range edges has implications for responses to multi-stressor environmental change, range edges also harboured alleles linked to SST not found, or found in very low frequencies, in central range populations. This suggests that low diversity has arisen through selection/local adaptation, which may be beneficial as the warm range edge is pushed against maximum thermal thresholds as ocean waters warm (Martinez et al., 2018). Predictions of genomic vulnerability showed that the high-diversity central range would be the most vulnerable under future climate change scenarios, as they likely lack alleles adapted to higher SST, and occur within one of the fastest warming regions globally. Together, these results suggest that interventions such as assisted adaptation and evolution will likely be warranted for this ecologically important species under future scenarios of climate change.

4.1 | Patterns of overall genetic diversity and structure

Our investigation revealed clear genetic clustering and differences in genetic diversity across *Phyllospora's* entire latitudinal range. This represents an advance on previous work that used microsatellites, mitochondrial and chloroplast markers, which only revealed weak patterns of genetic, and no haplotype or nucleotide, diversity across *Phyllospora's* central range (Coleman, Chambers, et al., 2011; Coleman et al., 2008; Durrant et al., 2015). Notably, range edges were clearly differentiated and only had approximately half the genetic diversity of the central populations. This pattern may be a result of smaller population sizes at range edges, limited connectivity or selection (Wernberg et al., 2018). These explanations are not mutually exclusive, and all may, in part, account for the observed patterns. For example, *Phyllospora's* connectivity is thought to be facilitated by large and abundant gas-filled floats that enable rafting and dispersal (Coleman et al., 2008; Coleman, Chambers, et al., 2011; although see Cole, 2017). Under a scenario of limited connectivity, high differentiation of populations at lower latitudes may be a result of prevailing ocean currents. The East Australian Current separation point is at ~31°S (around Forster, NSW), south of which eddies appear to facilitate greater dispersal and mixing, leading to less genetic structure (Coleman, Chambers, et al., 2011; Coleman, Roughan, et al., 2011). Connectivity patterns linked to the East Australian Current may therefore partly explain the relative distinctiveness of the only population north of this point (Port Macquarie), which also represents the rear range edge for the species. Similarly, the leading-edge Tasmanian populations (Bicheno and Southport) were also highly differentiated from the central range. This pattern may be due to recurrent bottleneck effects from reduced connectivity between mainland Australian and Tasmanian populations,

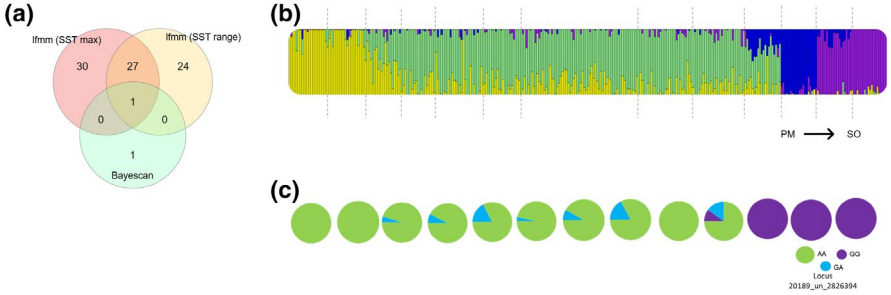


FIGURE 5 Single nucleotide polymorphism (SNP) loci putatively under selection across the *Phyllospora comosa* genome. (a) Venn diagram depicting overlaps between outlier loci detected using latent factor mixed models (*lfmm*) and *BayeScan* methods. Genetic structure of outlier loci detected within sample populations using (b) *lfmm* (overlapping sea surface temperature [SST] max and range) and (c) both *lfmm* and *BayeScan* shows greatest differences between range-edge and central populations. Pie charts depict allele frequencies at sample sites for the most significant outlier SNP, which was detected across all methods

which are separated by ~150 km of open ocean. Such patterns are largely congruent with connectivity patterns of other marine species in the region, which also show genetic structuring corresponding to the poleward flowing boundary currents (Coleman, Roughan, et al., 2011; Wernberg et al., 2013) and historic biogeographic isolation (Waters, 2008).

The high genetic differentiation exhibited at *Phyllospora's* warm range-edge population (Port Macquarie, NSW), along with significant deviations from HWE in 50% of loci at this site, is suggestive of non-random mating or small population size. This may suggest that the patterns of differentiation may be due to genetic drift, which is difficult to differentiate from selection with the current data. However, this population was unusual in that it was characterised by a very high proportion of males (80% compared to an average of 42% across the other sites). This sex bias may be a result of differential survival of male and female individuals as a result of temperature stress or other stressors associated with their marginal habitat. Under future climates, dioecious seaweeds are expected to exhibit sex bias towards males which show less sensitivity to change relative to females, which invest more heavily in reproduction (Hultine et al., 2016). Indeed, the pattern for potential selection which was emphasised in the northern rear-edge populations may have a sex bias with potential selection for longer survival of male plants under warmer waters. As we only sampled 20 individuals in this site, further sampling is needed to robustly assess sex ratios and manipulative experiments will be needed to thoroughly test any hypotheses regarding sex-based (or other) selection.

4.2 | Genomic links to current and future climate

We found evidence that *Phyllospora's* genomic diversity is linked to SST patterns along the coast, which may indicate local adaptation. This was further evidenced by the identification of potential SST-linked adaptive loci in range-edge populations (using LFMM), although results indicating whether adaptive loci were differentiated in northern range-edge and central populations varied between methods (LFMM vs. *BayeScan*). Crucially, associations with SST in the northern range edge may link to thermal tolerance, which is a hereditary trait that can vary among genotypes on similar spatial scales for other fucoid algae (Clark et al., 2013; Miller at al., 2020; although see Bennett et al., 2015). Both the GDM model and clustering analysis of the loci potentially under selection suggest that functional differentiation is relatively high and occurs between both range-edge and central populations. This subsequently renders the high diversity, central range as potentially the most vulnerable to the ocean warming that will characterise future oceans. However, given the relatively low number of loci used in this study, difficulties in teasing apart genetic drift and selection, and the fact that SST varies along a latitudinal gradient—along which many other environmental variables co-vary (e.g. nutrients, day length)—the driving factor(s) behind these potential patterns of selection remain unresolved and need to be established via experimental manipulations.

4.3 | Informing assisted evolution

Our results have clear implications for future management and conservation of this key forest-forming seaweed. Warming is a significant threat to *Phyllospora* populations, with the East Australian Current continuing to intensify, penetrate and separate further south (Cetina-Heredia et al., 2014). The underlying patterns of genetic variation we describe here may affect the response of this key forest-forming species to future stressors, leading to loss that is faster or occurs at larger scales than previously predicted. Future research to preserve genetic diversity (e.g. genebanks) and assess potential effects of assisted evolution strategies is critical to prevent the loss of populations and subsequent severe ecological effects in south-east Australia (Coleman & Wernberg, 2020; Coleman, Wood, et al., 2020; Wood et al., 2019, 2020).

A mixture of genetic diversity, identity and phenotypic plasticity will likely play a large role in determining which individuals survive under gradual ocean warming (McCoy & Widdicombe, 2019) and other potential stressors. Although our GDM models focused on temperature variables, limited genetic diversity (whether due to selection or drift) may limit overall adaptive capacity of range-edge populations and render them vulnerable to a variety of non-climate stressors to which they may be maladapted. For example, pollution and decreased water quality are also a threat to *Phyllospora* (Burridge et al., 1995) and were likely responsible for its historical decline around Sydney, Australia's largest city, located in the central range of the species' distribution (Coleman et al., 2008). Areas with the greatest pollution risk are likely to occur in the more populated regions near Sydney, where genetic diversity was also greatest, suggesting that there may be some adaptive capacity to cope with this stressor—although historical declines suggest this has its limits (Coleman et al., 2008).

While careful planning and long-term studies of potential genetic and ecosystem effects of interventions such as assisted evolution are vital, these must also be considered alongside the risks of no action (Filbee-Dexter & Smajdor, 2019; Weeks et al., 2011). To avoid wasting resources and potential risks of interventionist strategies, it is essential to consider the likelihood of adapted phenotypes being spread naturally to determine if interventionist strategies such as genetic rescue are truly necessary. Modelling predicted patterns of natural dispersal from genetically desirable populations to vulnerable populations under ecologically relevant timescales (e.g. Quigley et al., 2019) is thus a critical next step when deciding whether to intervene.

4.4 | Conclusion

Restoration and future-proofing programs have become urgent on a global scale (IPBES, 2019; IPCC, 2019) and the topic of how to appropriately utilise our understanding of genetic resources to mitigate climate change effects is receiving increasing attention, particularly in terrestrial and coral reef systems (Prober et al., 2015;

Rossetto et al., 2019; van Oppen et al., 2017). Given current efforts to restore *Phyllospora* across 70 km of Sydney's coastline correspond to areas with the highest estimates of genomic vulnerability over the next century, increasing warm-adapted allele frequencies in the central range may increase the resilience of restored areas to ocean warming. Additionally, this provides a testing ground for seaweed climate-provenancing strategies in a relatively isolated context. However, these actions clearly also need to be combined with other management strategies to limit individual and synergistic stressors, first and foremost—carbon emission reduction.

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DATA AVAILABILITY STATEMENT

Sampling locations and raw SNP genotypes/sequence data are available from the Digital Dryad Repository at https://doi.org/10.5061/dryad.2jm63xsnt.

ORCID

Georgina Wood https://orcid.org/0000-0003-3855-0932
Ezequiel M. Marzinelli https://orcid.org/0000-0002-3762-3389
Adriana Vergés https://orcid.org/0000-0002-3507-1234
Melinda A. Coleman https://orcid.org/0000-0003-2623-633X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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