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Climate adaptation and vulnerability of foundation species in a global change hotspot

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Abstract

Climate change is altering species ranges, and relative abundances within ranges, as populations become differentially adapted and vulnerable to the climates they face. Understanding present species ranges, whether species harbour and exchange adaptive variants, and how variants are distributed across landscapes undergoing rapid change, is therefore crucial to predicting responses to future climates and informing conservation strategies. Such insights are nonetheless lacking for most species of conservation concern. We assess genomic patterns of neutral variation, climate adaptation and climate vulnerability (offsets in predicted distributions of putatively adaptive variants across present and future landscapes) for sister foundation species, the marine tubeworms *Galeolaria caespitosa* and *Galeolaria gemineoa*, in a sentinel region for climate change impacts. We find that species are genetically isolated despite uncovering sympatry in their ranges, show parallel and nonparallel signals of thermal adaptation on spatial scales smaller than gene flow across their ranges, and are predicted to face different risks of maladaptation under future temperatures across their ranges. Our findings have implications for understanding local adaptation in the face of gene flow, and generate spatially explicit predictions for climatic disruption of adaptation and species distributions in coastal ecosystems that could guide experimental validation and conservation planning.

KEYWORDS
climate change, genetic offset, genomic vulnerability, genotype–environment association, seascape genomics, thermal adaptation

1 | INTRODUCTION

Global climate change is redistributing Earth's biodiversity. Geographical ranges are shifting as species move to track tolerable climatic conditions, and abundances are changing within ranges as populations adapt, or grow maladapted and thereby vulnerable, to the climates they face (Pecl et al., 2017; Scheffers et al., 2016). Understanding current ranges, whether species harbour (and exchange) different genetic variants involved in climate adaptation, and how such variants are distributed across landscapes undergoing rapid climate change, is therefore key to predicting responses to future change and informing conservation strategies (Teixeira & Huber, 2021; Willi et al., 2022). This remains challenging for many species, especially those that are cryptic or unsuited to traditional

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ways of inferring adaptation and persistence (reciprocal transplants, multigeneration breeding experiments, etc.). However, emerging tools linked to the rise of population genomic approaches for nonmodel organisms in recent years can provide new insights into climate adaptation and vulnerability for understudied species of conservation concern (Hoffmann et al., 2021; Hohenlohe et al., 2021).

Genomic predictions of climate adaptation rely on genome scans and genotype–environment associations to identify putatively adaptive (candidate) loci harbouring variants whose frequencies covary spatially with climate (Forester et al., 2016; Rellstab et al., 2015). Then, using climate forecasts, climate-adaptive candidates can be projected through time to assess the mismatch in their predicted distributions across present and future landscapes, known as genetic offset (Capblancq et al., 2020; Fitzpatrick & Keller, 2015) or genomic vulnerability (Hoffmann et al., 2021). Such assessments assume that candidate loci have causal effects on fitness, which is challenging to validate, and ignore the scope for phenotypic plasticity or future adaptation to temper vulnerability (Hoffmann et al., 2021; Láruson et al., 2022; Rellstab et al., 2021). Nevertheless, they offer promising tools for identifying regions in which taxa of ecological importance, but limited tractability to experimentation, may be at risk of decline without adaptation in situ to track future climates, and for identifying key environmental drivers of that risk (Fitzpatrick et al., 2021; Láruson et al., 2022). Combining such assessments with insights from neutral genomic variation, moreover, may allow population structures and species barriers to be explored from adaptive and nonadaptive perspectives, with differing implications for population dynamics, species range shifts and management actions under climate change (Hohenlohe et al., 2021; Kardos et al., 2021; Willi et al., 2022).

Accordingly, mounting studies have now assessed genomic vulnerability to climate change for large, long-lived or otherwise intractable species, including trees (Borrell et al., 2020; Ingvarsson & Bernhardsson, 2020; Jia et al., 2020; Pina-Martins et al., 2019), seaweeds (Vranken et al., 2021; Wood et al., 2021) and birds (Bay et al., 2018). Rarely, however, has the approach been extended to related species in overlapping ranges (but see Nielsen et al., 2021), despite the predicted impacts of dispersal and gene flow not only among populations but also across species barriers that remain permeable. The extent of local adaptation reflects the balance between migration and selection (Savolainen et al., 2013; Yeaman & Otto, 2011). Locally beneficial variants can establish and persist if selection is strong relative to migration, but should be swamped by gene flow or lost to drift otherwise (García-Ramos & Kirkpatrick, 1997; Haldane, 1930; Lenormand, 2002). Gene flow across species barriers can create highly fit hybrids that increase population sizes in the short term (Fitzpatrick et al., 2020) or rates of adaptation in the long term (Grant & Grant, 2019; Mitchell et al., 2019). Conversely, it may introduce variants into new environments to which they are maladapted (Hoffmann & Sgrò, 2011; Polechová, 2018), or cause outbreeding depression if species' genomes are incompatible (Frankham, 2015). Over time, species barriers may blur or vulnerable species may be displaced by less vulnerable ones, at a net cost to biodiversity (Román-Palacios & Wiens, 2020; Todesco et al., 2016). Multispecies assessments of genomic vulnerability may thus help to identify genetic lineages on distinct evolutionary pathways linked to climate, which could warrant separate management to conserve their genetic uniqueness (Willi et al., 2022).

Gaps also limit our understanding of adaptation and vulnerability to different components of climate change, given signs of change in not only the means (or trends) of key variables, but also their extremes and the extents to which they vary predictably or stochastically (Fischer & Knutti, 2015; Ruokolainen et al., 2009; Waldock et al., 2018). By imposing different selective pressures, these components may have different consequences for biodiversity and lead to different risks of fitness decline (Bitter et al., 2021; Kingsolver & Buckley, 2017; Lande, 2014; Rescan et al., 2021; Ripa & Lundberg, 1996). To date, however, most assessments of climate adaptation have focused on variables (precipitation, temperature, vegetation, elevation) relevant to terrestrial systems, whereas marine systems are underrepresented (Grummer et al., 2019; Lotterhos et al., 2021). Compared to terrestrial species, marine species often have high fecundity, large population sizes and extensive dispersal at early life stages (gametes, embryos and larvae) with high mortality, especially when development is planktonic (Plough, 2016; Strathmann, 1990). Gene flow, selection and drift can therefore play out in oceanographic settings that strongly couple physical and evolutionary processes, while decoupling the environments of early stages and adults (Lotterhos et al., 2021). Trends in key variables such as temperature, moreover, are less striking and stable than they are on land (Gaylord & Gaines, 2000), potentially giving other components of change (e.g., extremes or predictability) greater influence. Marine systems can therefore offer new genomic insights into adaptation, especially in the face of gene flow (Liggins et al., 2019; Tigano & Friesen, 2016). Nevertheless, assessments of genomic vulnerability to climate change remain rare, especially in marine systems (but see Vranken et al., 2021; Wood et al., 2021), have not explored environmental drivers such as predictability and are lacking for many species of ecological importance in regions undergoing rapid change where adaptation may be vital for persistence.

Southeast Australia is a climate change hotspot, identified as one of the world's fastest warming marine regions and also one of its most biodiverse (Hobday & Pecl, 2014; Ramírez et al., 2017). East–west differentiation of lineages in the region is often attributed to historical isolation by a land-bridge joining Tasmania and mainland Australia during glacial maxima (Dawson, 2005; O'Hara & Poore, 2000). The region also sees two boundary currents—the East Australian Current flowing south from the tropics, and the Zeehan Current flowing east from the Great Australian Bight—meet subantarctic water in Bass Strait. Both currents vary seasonally, with the former strongest in summer and the latter strongest in winter (Ridgway, 2007), forming complex gradients in temperature and flow that may shape postglacial gene flow, selection and drift (Miller et al., 2020; Waters, 2008). Those gradients are set to steepen as the East Australian Current continues to warm and intensify southward (Hobday & Lough, 2011; Ridgway & Hill, 2009), making the region a natural laboratory for

studying climate adaptation and vulnerability in order to better predict how biodiversity will fare in future climates.

Here, we assess climate adaptation and vulnerability in the endemic marine tubeworm *Galeolaria*, a genus of sessile, habitat-forming foundation species that enhance coastal biodiversity (Cole et al., 2018; Wright & Gribben, 2017). In the southeast hotspot, two cryptic sister species are geographically concordant with neutral genetic markers that place *G. gemineoa* at warmer, northern latitudes and *G. caespitosa* at cooler, southern ones (Halt et al., 2009). Species have high dispersal capacity in early life and may still cross-fertilize (Styan et al., 2008), yet their ranges, the extent of gene flow within and between species, and whether species are locally adapting to climate within the spatial scale of gene flow is unknown. Thus, we ask whether sister *Galeolaria* species show signals of climate adaptation despite potential gene flow, whether signals are similar or divergent between species, and whether species differ in genomic vulnerability to climate change. To address these questions, we first characterize spatial patterns of gene flow and genetic differentiation within and between species throughout the hotspot. Second, we identify candidate loci displaying signals of climate adaptation (specifically, to different components of temperature) in each species, and combine candidate loci with climate forecasts to predict each species' genomic vulnerability to ongoing climate change. Our analyses suggest that sister species are now partly sympatric in the hotspot but do not appear to hybridize, show a blend of parallel and unique signals of local adaptation to climate in the face of extensive gene flow, and are differentially vulnerable to near-future climates. Our study has fundamental implications for understanding adaptation with gene flow, and provides insights into evolutionary processes that could be used to better manage and conserve biodiversity in a sentinel region for climate impacts.

2 | METHODS

2.1 | Study system

Galeolaria tubeworms are foundation species on rocky shores of southeast Australia, where their dense colonies of stony tubes enhance coastal biodiversity by providing habitat and refuge from environmental stressors for species that cannot otherwise persist there (Figure 1a; Cole et al., 2018; Wright & Gribben, 2017). Year-round, adults shed gametes into the sea for external fertilization and embryogenesis (Chirgwin et al., 2020, 2021). Larvae then spend another ~2–3 weeks offshore, dispersed by currents, before transitioning to sessile life stages (juveniles and adults) onshore in the intertidal zone. As for other aquatic ectotherms, planktonic stages are thermal bottlenecks in the life cycle, defining vulnerability to climate as well as gene flow and genetic differentiation across species' ranges (Dahlke et al., 2020; Lotterhos et al., 2021; Rebolledo et al., 2020). *Galeolaria caespitosa* and *G. gemineoa* are said to have diverged in the hotspot due to historical isolation or restricted dispersal across unsuitable habitat (90 Mile Beach; Figure 1b), with *G. caespitosa* occurring west to Western Australia and *G. gemineoa* occurring north to Queensland (Halt et al., 2009; Styan et al., 2008).

2.2 | Sampling throughout the southeast Australian hotspot

We sampled adult populations of *G. caespitosa* and *G. gemineoa* from 30 locations spanning ~800 km of coast throughout the hotspot (Figure 1b; Table S1) in January 2019. Locations were chosen to capture thermal variation in each species' range based on preliminary analyses of sea-surface temperature data. We aimed to sample every 20 km of coastline, but distance between locations sometimes ranged from 7 to 200 km subject to accessibility and species detection (see Figure 1b). Each of 10–15 individuals per location was immediately extracted from its tube, spawned for 5 min in filtered seawater to minimize contamination by gametes, then rinsed and placed in an Eppendorf tube with 70% ethanol. Individuals were transported to the laboratory and stored at room temperature (~22°C) until DNA extraction.

2.3 | DNA extraction, library preparation and sequencing

We extracted DNA from the posterior ~5 mm of each individual. We digested tissue overnight with proteinase K, then extracted DNA using the Qiagen DNeasy Blood and Tissue Kit following the manufacturer's instructions (Qiagen, 2006). Quality was checked by running individual samples on 2% agarose gel stained with ethidium bromide and also with a UV–Vis spectrometer (NanoDrop 1000, Thermo Scientific). Quantity was checked with a QuBit fluorometer (dsDNA HS, Invitrogen).

Library preparation followed a double-digest genotyping-by-sequencing protocol, using *Pst*I-HF and *Msp*I restriction enzymes and equal amounts of DNA per individual (Poland et al., 2012). Both enzymes are methylation-sensitive and may therefore enrich for genic regions of the genome (Pootakham et al., 2016). The extent of DNA methylation in our species is unknown, but was detected at 63%–73% of scorable loci in a close relative (Ardura et al., 2017). The protocol was modified by performing PCR (polymerase chain reaction) amplifications for individuals, then pooling equal amounts of PCR products. A size selection step targeting 400–600-bp fragments was also added to ensure repeatable sampling of comparable subsets of the genome across individuals and species (Andrews et al., 2016; Peterson et al., 2012). Sequencing was performed in two batches, one by GenomeQuébec and one by GENEWIZ. Both batches used one lane of Illumina HiSeq 4000 (paired-end, 150 bp). Data are archived in Gallegos et al. (2022).

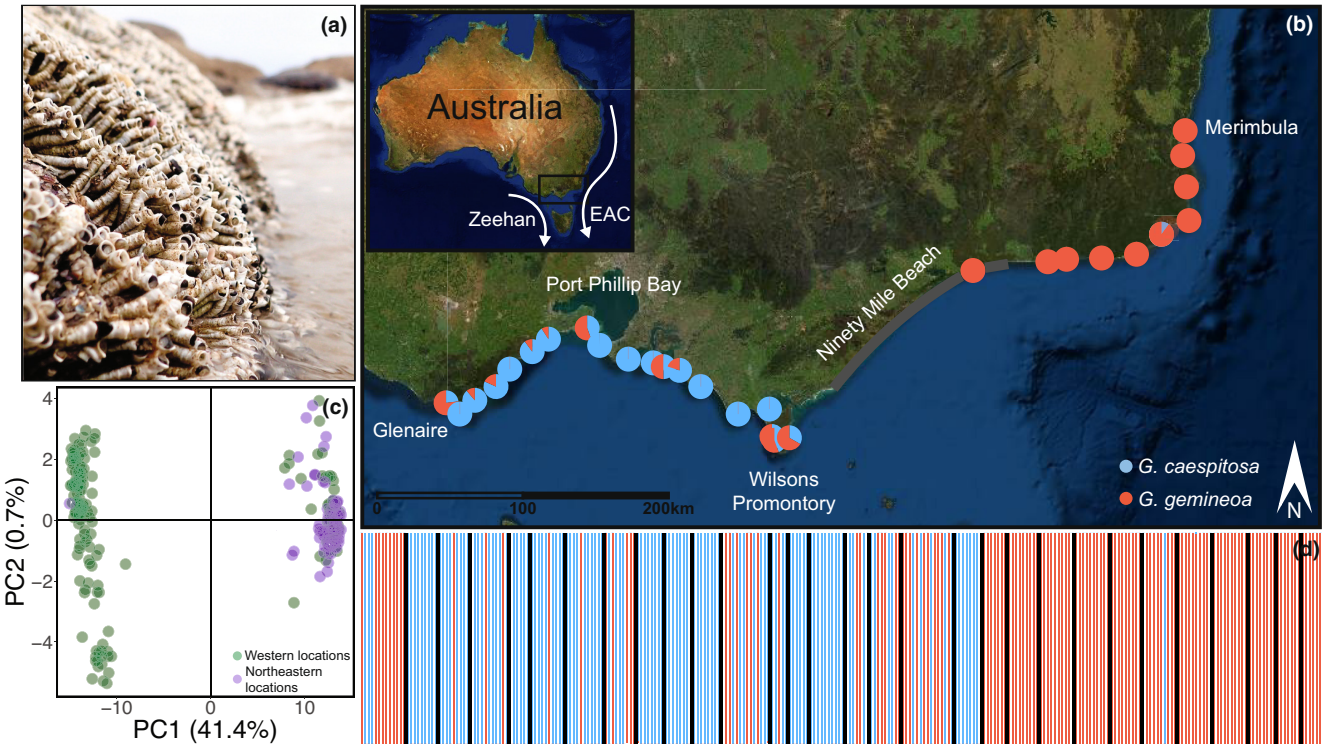

FIGURE 1 Geographical setting and genetic structures of *Galeolaria* species. (a) A typical colony showing adults retracted into tubes at low tide. (b) Locations from which species were sampled across the hotspot, where boundary currents converge at a now-submerged land bridge between Tasmania and mainland Australia (inset). Pie charts show the proportions of individuals identified as *Galeolaria caespitosa* (blue) and *G. gemineoa* (red) by ADMIXTURE analyses. Until now, species ranges were thought to diverge near Ninety Mile Beach (grey line), which lacks rocky habitat to colonize. (c) A principal components analysis of genetic variation reveals two distinct clusters corresponding to the two species, with individuals from western locations (Glenaire to Wilsons Promontory) in green and individuals from northeastern locations (Wilsons Promontory to Merimbula) in purple. (d) Ancestries of individuals (vertical bars, coloured as in (a)) suggest little gene flow between species. Vertical black lines group individuals by location.

2.4 | Identifying single nucleotide polymorphisms (SNPs)

Raw reads were quality-checked using FASTQC (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/), then demultiplexed and cleaned using process_radtags in the STACKS software pipeline (Catchen et al., 2011; Catchen et al., 2013). To optimize parameter values for identifying SNPs, we ran the pipeline nine times using a range of values for a subset of 16 individuals, then explored key statistics including the distribution of SNPs per locus and the number of loci shared by at least 80% of individuals (Paris et al., 2017; Rochette & Catchen, 2017). Based on results, we called SNPs for all individuals using values of $m = 3$, $M = 5$ and $n = 5$, where m is the minimum number of raw reads required to form a stack (a putative allele), M is the number of mismatches allowed between stacks to merge them into a putative locus, and n is the number of mismatches allowed between stacks during construction of the catalogue (representing homologous loci across individuals; Paris et al., 2017).

We filtered SNPs in several steps. First, we filtered loci with low allele frequencies in STACKS (with min_maf = 0.01). Next, we filtered the remainder in VCFR version 1.8.0 (Knaus & Grünwald, 2017), ADEGENET version 2.1.1 (Jombart, 2008) and GASTON version 1.5.6 (Perdry & Dandine-Roulland, 2020) to keep only biallelic loci with depth >5 and genotype quality >30, and to exclude individuals missing more than 60% of loci. Last, we excluded loci missing more than 55% of data across individuals and loci with linkage disequilibrium (r^2) > 0.8. We used this large SNP set for genotype–environment association analyses. For all analyses of population genetic structure, which do not require large numbers of SNPs, we used a reduced SNP set that excluded loci missing more than 30% of data across individuals.

Remaining data analyses were performed in R version 4.0.5 (R Core Team, 2021) unless otherwise stated.

2.5 | Environmental data

With climate change, marine species face particular risks of extinction due to water warming and the ensuing loss of oxygen (Penn & Deutsch, 2022; Pinsky & Fredston, 2022). We therefore focused on assessing adaptation to different components of temperature, but acknowledge that other variables (e.g., water chemistry) may also drive adaptation in marine systems (Bitter

et al., 2019; Rautsaw et al., 2021). We obtained a high-resolution (1-km^2 grid cell) satellite-based time series of sea surface temperature from January 2010 to December 2018 (www.ghrsst.org), and extracted daily observations for all 30 locations. We summarized data using 10 variables based mostly on the WorldClim scheme (Fick & Hijmans, 2017; Hijmans et al., 2005), then selected four that captured different components of change in temperature and had pairwise correlations below |0.7| (Table S2). They were mean temperature (a measure of trend), maximum temperature of the warmest month (a measure of extremity), mean monthly temperature range (a measure of variability) and temperature noise structure (a measure of stochasticity; see Appendix S1 for calculations). Variables were mean-centred and scaled as recommended for subsequent analyses (Gautier, 2015).

2.6 | Analyses of population genetic structure

2.6.1 | Genetic clustering

To explore genetic differentiation within and between species, we estimated the ancestries of individuals, and levels of admixture among ancestral lineages, using ADMIXTURE version 1.3 (Alexander et al., 2009). The parameter K (presumed number of ancestral lineages) was set to 2 for the between-species analysis, which minimized cross-validation error. The latter was minimized at $K = 1$ for each within-species analysis, supporting only a single ancestral lineage per species. Setting higher values of K did not alter our results. We also clustered loci based on principal components analyses of genetic variation, using ADEGENET version 2.1.1 (Jombart, 2008). To compare the contributions of demographic history and climate adaptation to differentiation within species, clustering was done separately for putatively neutral vs. adaptive loci. The latter were identified for each species by genome scans of the large SNP set in BAYPASS version 2.3 (Gautier, 2015; see details below), while the former were loci in the reduced SNP set after adaptive loci were removed.

2.6.2 | Genetic diversity

To explore genetic diversity within species, and because some loci were polymorphic between species only, we filtered out loci that were monomorphic or unique to one species. For each population, we then calculated standard measures of diversity—observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) and allelic richness (AR)—averaged across loci in HIERFSTAT version 0.5–7 (Goudet & Jombart, 2015). We compared diversity between species using F-tests from linear models with species as a categorical fixed effect, and corrected for multiple testing by controlling the false discovery rate. Diagnostic plots of residuals detected no serious violations of model assumptions.

2.6.3 | Spatial genetic structure

To explore spatial genetic structure shaped by gene flow throughout species' ranges, we calculated the matrix of pairwise genetic distances (F_{ST}, also averaged across loci) among populations of each species in HIERFSTAT version 0.5–7 (Goudet & Jombart, 2015). Populations represented by fewer than three individuals were excluded from calculations to reduce sampling error (Nazareno et al., 2017). We then passed each matrix, along with population geographical coordinates, to the *mgQuick* function of MEMGENE version 1.0.2 (Galpern et al., 2014). The function identifies vectors of spatial variation in genetic distance (Moran's eigenvector maps, or MEMs; Legendre & Fortin, 2010) based on permutation tests of their significance. We used the function's default settings, but increased the number of permutations for identifying significant vectors to 1000.

2.7 | Analyses of climate adaptation and vulnerability

2.7.1 | Candidate loci for thermal adaptation

To identify candidate loci whose allele frequencies vary in association with temperature, we performed genome scans separately by species in BAYPASS version 2.3 (Gautier, 2015). First, we fitted the core (covariate-free) model to the reduced SNP set to estimate the population covariance matrix (Ω) of allele frequencies due to shared demographic history. Second, we fitted the auxiliary covariate model (with temperature variables and Ω jointly analysed as covariates) to the large SNP set to identify candidate loci while correcting for neutral population structure due to shared history. We used default settings, but increased the thinning interval and burn-in to 50 and 10,000, respectively, to ensure chain convergence (checked by running the model five times with different seeds, per the BAYPASS manual). Since all runs converged on similar results, we used the default run (seed = 5001) for further analyses. We identified candidate loci as allele frequency outliers based on p-values of XtX statistics (analogous to F_{ST}) and inferred associations with temperature variables based on Bayes Factors greater than 20 (decisive evidence of association) after correction for multiple testing (Gautier, 2015). We then tested whether more temperature-associated candidates overlapped between species than expected by chance due to sampling, given the numbers identified from those screened, using a one-tailed hypergeometric test.

2.7.2 | Genomic vulnerability to climate change

To assess species' vulnerability to climate change in the hotspot, we used gradient forests (Ellis et al., 2012; Fitzpatrick & Keller, 2015) to predict spatial turnover of alleles at temperature-associated candidate loci in current and future climates. Gradient

TABLE 1 Estimates of genetic diversity (mean ± *SE*) for *Galeolaria caespitosa* and *G. gemineoa*.

	H_O	H_E	F_{IS}	AR
Galeolaria caespitosa	0.067 ± 0.001	0.097 ± 0.001	0.212 ± 0.009	1.271 ± 0.016
Galeolaria gemineoa	0.059 ± 0.001	0.084 ± 0.001	0.210 ± 0.010	1.220 ± 0.020
	$F_{(1,40)} = 38.82^{**}$	$F_{(1,35)} = 152.61^{**}$	$F_{(1, 35)} = 0.20$	$F_{(1, 40)} = 4.70^{*}$

H_O is observed heterozygosity, H_E is expected heterozygosity, F_{IS} is the inbreeding coefficient and AR is allelic richness (ranging from one to two because only biallelic loci were analysed). Estimates are averaged across loci and populations (see Table S3 for population values) and compared between species using *F*-tests adjusted for multiple testing (*$p \leq .05$; **$p \leq .001$).

forests use a machine-learning algorithm to estimate turnover functions describing changes in allele frequencies along spatial gradients defined by predictors. Functions are weighted by predictor importance and model goodness-of-fit (R^2) for each candidate, with only candidates having $R^2 > 0$ retained (Fitzpatrick & Keller, 2015). This step therefore provides spatially explicit predictions about local adaptation, along with further screening of temperature-associated candidates. We fitted models separately by species with minor allele frequencies at candidate loci as response variables, temperature variables as predictors, and 2000 regression trees per locus using default settings in GRADIENTFOREST version 0.1–32 (Ellis et al., 2012).

To map current turnover for each species, we extracted temperature variables for each grid cell in the study range and transformed variables into genetic importance (relative importance to allele turnover) using the estimated turnover function (Fitzpatrick & Keller, 2015). We summarized transformed variables as three principal components, assigned components to an RGB colour palette following Ellis et al. (2012), then mapped colours to grid cells using RASTER version 3.5 (Hijmans, 2017). Mapped this way, colours predict genetic compositions (allele frequencies) in cells, and similar compositions are predicted for locations of similar colour. Biplots of the two largest principal components were used to relate turnover in composition to changes in temperature (Ellis et al., 2012).

Rather than map future turnover for each species directly, we translated it to the genetic offset predicted to maintain thermal adaptation under climate change (Ellis et al., 2012; Fitzpatrick & Keller, 2015). We repeated the process above with mean and maximum temperatures projected for 2050 and 2100 under low (RCP4.5) and high (RCP8.5) CO_2 emission scenarios, extracted for each grid cell from the Bio-ORACLE database (Assis et al., 2018; Tyberghein et al., 2012). Since projections for other variables were unavailable, we also recalculated current turnover without them. For each cell, we transformed variables into genetic importance as above, calculated genetic offset as the Euclidian distance between current and future genetic compositions, then mapped offset as above.

3 | RESULTS

3.1 | Variant identification

Sequencing returned an average of 3,392,340 quality-filtered reads per individual, with ~24-fold read depth on average. STACKS (Catchen et al., 2011) identified 8,887,109 putative SNPs from 330 individuals. Filtering retained 8788 unlinked loci from 272 individuals (with 16% of data missing across loci and individuals) for the reduced SNP set used to analyse population genetic structure, and 24,263 unlinked loci from 272 individuals (with 31% of data missing across loci and individuals) for the large SNP set used to analyse genotype–environment associations. Since the genome size is ~707 Mb (K. Hodgins and K. Monro, unpublished data), we were able to interrogate a locus for signals of thermal adaptation approximately every 29 kb on average.

3.2 | Analyses of population genetic structure

3.2.1 | Genetic clustering

Principal components analysis of genetic variation in the reduced SNP set revealed two distinct genetic clusters defined by PC1 and PC2, jointly accounting for 42.1% of the variation sampled (Figure 1c). Most individuals in one cluster were from northeastern locations, whereas most individuals in the other cluster were from western ones (Figure 1b). However, multiple individuals from western locations clustered with the "northeastern" cluster, and one individual from a northeastern location clustered with the "western" cluster (Figure 1c).

ADMIXTURE analyses supported the presence of individuals from different ancestral lineages in western and northeastern populations (Figure 1b,d), but detected little gene flow between lineages (individual ancestry proportions consistently exceeded 0.99, seen as single-coloured bars in Figure 1d). Based on existing knowledge of species distributions (Halt et al., 2009), the "northeastern" cluster represents *Galeolaria gemineoa* and the "western" cluster *G. caespitosa*, but species are now shown to be sympatric in some locations, especially those in the west of the hotspot (Figure 1b). Subsequent analyses were therefore separated by species based on ADMIXTURE assignments. We also used the reduced SNP set to explore genetic clustering or signs of distinct lineages within species, but detected none in either case (Figure S1A,B).

3.3 | Genetic diversity

Roughly 30% of loci in the reduced SNP set were polymorphic and shared between species. On average, measures of genetic diversity based on these loci were significantly lower for *G. gemineoa* than

for *G. caespitosa*, except for inbreeding coefficients (Table 1). These were similarly high (~0.21) for both species, indicating that populations harbour more homozygotes than expected under Hardy–Weinberg equilibrium.

3.3.1 | Spatial genetic structure

Within species, mean (±SE) pairwise genetic distance (F_{ST}) based on the reduced SNP set was relatively low (*G. caespitosa*: 0.066±0.001; *G. gemineoa*: 0.062±0.001; see Figure S2 for all values), but significantly lower for *G. gemineoa* ($F_{(1,305)}$ =6.567, p <.02). No vectors of spatial variation in genetic distance (MEMs) were significant for either species (R^2 ≈0, p ≈1 in each case), indicating a lack of spatial genetic structure consistent with gene flow across their ranges in the hotspot.

Between species, in contrast, mean pairwise genetic distance (F_{ST}) was relatively high (0.599±0.008), offering more evidence of their genetic differentiation. To further check whether species remain differentiated in sympatry, we compared mean species-level F_{ST} between sympatric and allopatric populations (see Figure S3 for all values). No difference was detected (F_{ST} in sympatry: 0.599±0.009; F_{ST} in allopatry: 0.598±0.001; $F_{(1,85)}$ =0.015, p =.903), suggesting that species barriers persist even when geographical barriers are absent.

3.4 | Analyses of climate adaptation and vulnerability

3.4.1 | Candidate loci for thermal adaptation

Genome scans of the large SNP set identified 1736 XtX outlier loci for *G. caespitosa* and 1388 such loci for *G. gemineoa*. Based on support from Bayes factors, those identified for *G. caespitosa* were mostly associated with mean temperature (41), while 11 were associated with maximum temperature, nine with temperature range and seven with temperature noise structure. Those identified for *G. gemineoa* were mostly associated with mean temperature (16) and temperature range (16), while five were associated with maximum temperature and four with temperature noise structure (Figure 2 and Table S4). Species shared 9%–17% of all temperature-associated candidates, which was significantly more than expected by chance due to sampling (p <.001; Figure 3) and suggests a blend of parallel and nonparallel adaptation. Note that candidate numbers in Figure 3 are less than the sums of numbers above due to some associations with multiple variables.

In contrast to clustering of neutral loci, clustering of putatively adaptive loci revealed stronger population differentiation within species (for *G. gemineoa* especially), with western populations tending to cluster separately from those further northeast (Figure S1C,D).

3.4.2 | Genomic vulnerability to climate change

Gradient forests predicted spatial turnover in allele frequencies at 12 temperature-associated candidate loci (from 64 screened) in *G. caespitosa*, and 16 temperature-associated candidate loci (from 35 screened) in *G. gemineoa* (Figure S4). While all temperature variables contribute to estimated turnover functions, noise structure and maximum were most important to turnover in *G. caespitosa*, whereas mean and range were most important to turnover in *G. gemineoa* (see importance rankings in Figure S5).

Mapping current turnover within species predicted greater shifts in putatively adaptive variants along the open coast for *G. gemineoa* than for *G. caespitosa* (Figure 4), in line with patterns of population

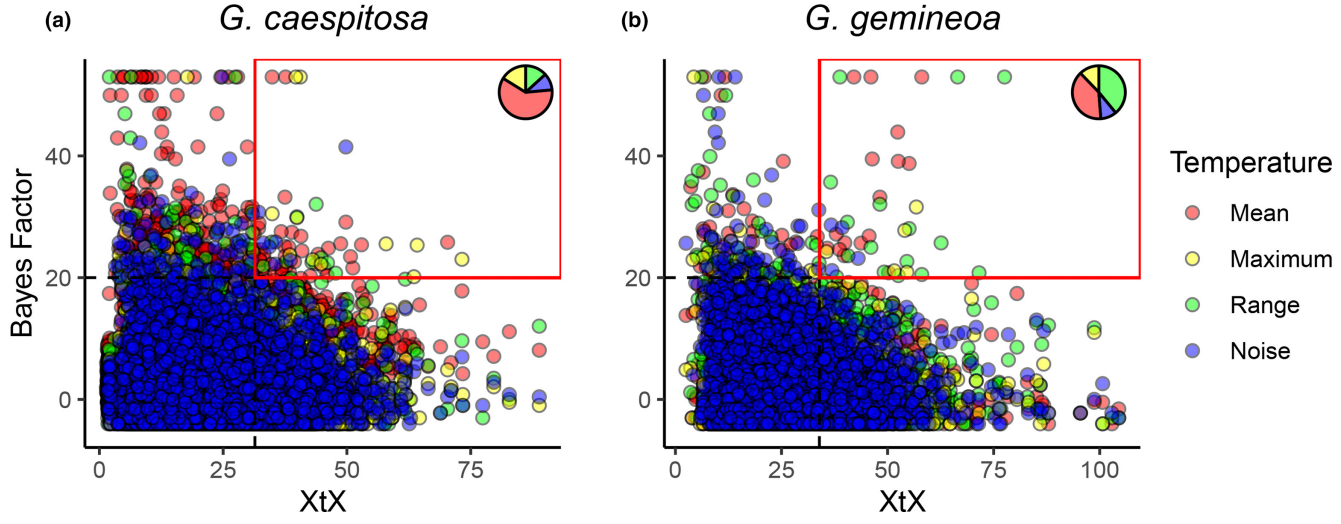

FIGURE 2 Associations between loci (points) and temperature variables (mean, maximum, range and noise structure) identified for (a) *Galeolaria caespitosa* and (b) *G. gemineoa* by genome scans in BAYPASS. Candidate loci are those with XtX statistics above vertical dashed lines (indicating $p \leq .05$). Loci associated with temperature variables are those with Bayes factors above horizontal dashed lines (indicating decisive evidence of association; Gautier, 2015). Candidate loci for thermal adaptation (in red squares) meet both conditions, and are coloured by the variable they associate with. Pie charts show the proportions of candidates associated with different variables.

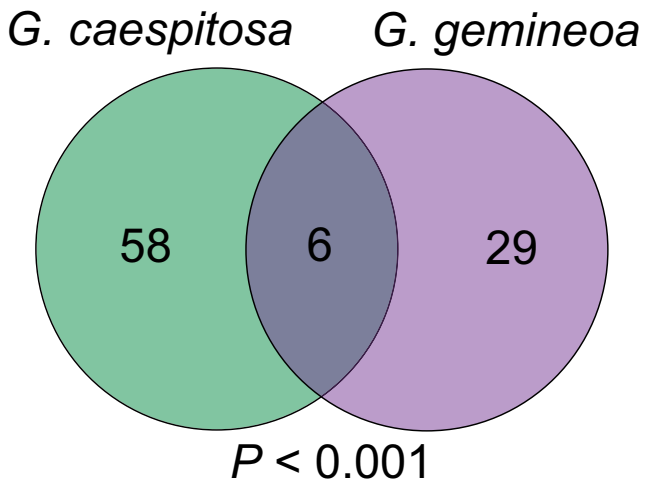

FIGURE 3 Overlap of temperature-associated candidate loci between *Galeolaria caespitosa* and *G. gemineoa*, supporting a blend of parallel and nonparallel adaptation. Species share 9%–17% of candidate loci, which is significantly more than expected by chance given the number of candidates identified from the total number of loci screened.

structure in putatively adaptive loci (Figure S1C,D). For *G. caespitosa*, little turnover was predicted except between western populations and the sole northeastern sample, associated with changes in mean and maximum temperature (higher in more purple and teal parts of the range respectively; Figure 4a,b). For *G. gemineoa*, comparatively greater turnover was predicted between western (sympatric) populations and northeastern (allopatric) populations, associated with changes in temperature mean and range (higher in more purple and green parts of the range respectively; Figure 4c,d). For both species, turnover was also predicted between the coast and enclosed bays, associated with changes in temperature noise structure and range (both higher in bays).

Unsurprisingly, more extreme warming (RCP4.5 vs. RCP8.5 and 2050 vs. 2100 scenarios) is predicted to increase divergence between current and future allele frequencies in both species, and hence the genetic offset they need to maintain thermal adaptation (Figure 5). For *G. caespitosa*, the predicted offset varied little across the hotspot, but was highest in the northeast (Figure 5a). For *G. gemineoa*, the predicted offset was roughly double that for *G. caespitosa* and markedly higher for western (sympatric) populations compared to northeastern (allopatric) ones, though this difference may fade under more extreme warming in the longer term (Figure 5b).

4 | DISCUSSION

With climate change redistributing biodiversity around the globe (Pecl et al., 2017), predicting species' responses to future climates entails understanding their current ranges, whether they harbour or share genetic variants involved in climate adaptation, and how variants are distributed across ranges undergoing climate change. We assessed the distributions of neutral and adaptive genomic variation in sister foundation species—the marine tubeworms *G. gemineoa* and *G. caespitosa*—across a sentinel region for climate impacts. We found that species are genetically isolated despite uncovering sympatry in their ranges, show parallel and nonparallel signals of thermal adaptation despite seemingly high gene flow across their ranges, and are predicted to face different risks of maladaptation under forecasted temperatures across their ranges. Our results have implications for understanding genetic parallelism and the maintenance of species barriers in the face of gene flow, and generate spatially explicit predictions for climatic disruption of adaptation and species distributions in coastal ecosystems that could guide experimental validation and conservation planning.

Detection of sympatry in sister *Galeolaria* species updates previous molecular support for their geographical isolation (Halt et al., 2009; Styan et al., 2008), and could reflect poleward range expansion (as reported for other marine species in the hotspot during the last decade; Sunday et al., 2015) or else more intensive sequencing across the hotspot here than in previous work. That species apparently coexist without admixture, despite their partial capacity to cross-fertilize (Styan et al., 2008), points to isolation by extrinsic prezygotic barriers (e.g., spawning asynchrony, conspecific sperm precedence; Howard, 1999; Lotterhos & Levitan, 2010) or postzygotic selection against hybrids (Fierst & Hansen, 2010; Sinervo & Calsbeek, 2003), and such possibilities warrant further research to understand the maintenance of species barriers in warming seas. That species also have higher-than-expected levels of inbreeding, despite little evidence of neutral population structure across their ranges, may be typical of external fertilizers with dispersive propagules and limited control of mate choice, and is attributed to chronically low effective population sizes driven by high variance in reproductive success (Olsen et al., 2020; Plough, 2016). Other measures of neutral diversity were lower in *G. gemineoa* than in *G. caespitosa*, however, suggesting that differing demographic histories (e.g., population bottlenecks or range expansion) have left one species more genetically depauperate, and potentially more vulnerable to decline, than the other (Reed & Frankham, 2003; Sgrò et al., 2011).

For both *Galeolaria* species, population structure in temperature-associated candidate loci, in the absence of neutral structure, suggests that populations are adapting to climate in the face of gene flow across their ranges (Tigano & Friesen, 2016). In theory, this is unlikely to occur unless selection is strong enough for locally beneficial variants to establish and resist swamping by migrants (Lenormand, 2002; Yeaman & Otto, 2011), selection targets large-effect variants with more resistance to swamping (Yeaman & Otto, 2011; Yeaman & Whitlock, 2011), or variants are selected elsewhere in species' ranges before migrating to local populations (Barrett & Schluter, 2008). Our spatial modelling predicts different compositions of temperature-associated variants in different parts of species' ranges (e.g., western vs. northeastern locations), but all such variants have been filtered by selective forces correlated with temperature-related variables to some degree. It is therefore plausible that introgression of thermally pre-adapted variants may be

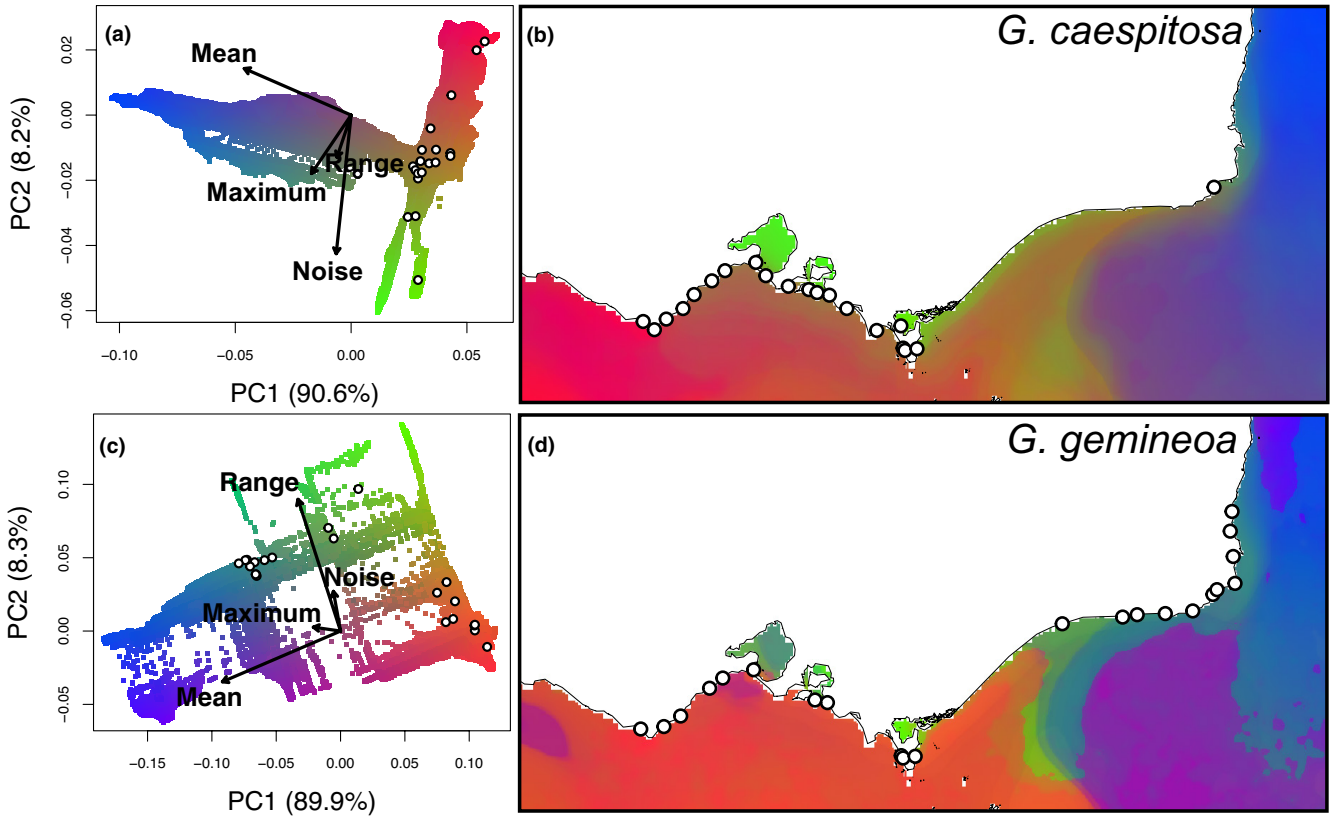

FIGURE 4 Temperature-associated turnover in allele frequencies at candidate loci predicted for (a,b) *Galeolaria caespitosa* and (c,d) *G. gemineoa* by gradient forests. Biplots in (a) and (c) show the two largest principal components (PC1 and PC2) per model, comprising linear combinations of temperature variables (mean, maximum, range and noise structure) that explain 98%–99% of turnover per species. Colours predict turnover along biplot axes, and vectors relate turnover to variables (variables increase in the directions of vectors, contribute more to turnover if vectors are longer and have correlated effects if vectors align). Maps in (b) and (d) predict turnover throughout the study range, with similar allele frequencies predicted for locations of similar colour. Points are locations from which species were sampled. Species have planktonic life stages (gametes, embryos and larvae) that spend days to weeks offshore before transitioning to sessile stages (juveniles and adults) onshore in the intertidal zone.

countering the swamping effects of migration within species (Tigano & Friesen, 2016), although our molecular data are consistent with strong species boundaries even in sympatric populations. However, this, and the possibility of large-effect variants contributing to adaptation with gene flow, await testing with more extensive genomic resources than were available here.

Evidence that *Galeolaria* species share more temperature-associated candidates than expected by chance supports a mix of parallel and nonparallel adaptation between lineages. Thermally adapted variants at the same loci in both species could emerge from selection on standing genetic variation in their ancestor, admixture not detected by our analyses or independent mutations (Lee & Coop, 2017; Stern, 2013; Wood et al., 2005). Nevertheless, such overlap supports the idea that these loci are involved in adaptation, since the same false positives are unlikely to be identified in both lineages, particularly if mutations were independently derived in them (Yeaman et al., 2016). That most candidates were species-specific, however, could have several nonmutually exclusive explanations. First, species may be responding to divergent thermal selection, given that *G. gemineoa* spans a wide latitudinal range (Halt et al., 2009) and more of its adaptive genetic turnover is associated with mean temperature, whereas *G. caespitosa* spans a narrower range with more complex hydrodynamics (Waters, 2008) and more of its adaptive turnover is associated with stochastic changes in temperature. Second, species may face similar selection, but differ genetically in ways that favour the detection of nonparallelism between them (Blount et al., 2018; Lenormand et al., 2016). Since thermal adaptation is polygenic, and species were isolated historically (Halt et al., 2009; Styan et al., 2008), this hypothesis is highly likely here. Third, nonparallelism may reflect incomplete sampling of the genome, given our reliance on reduced representation sequencing to identify candidates. The cost-effectiveness of this approach, however, permitted larger sample sizes that enhance power to detect selection at genotyped loci in both species, and sequencing to higher read depths that reduce errors in genotyping and allele frequency estimation (Andrews et al., 2016; Hoban et al., 2016). This should increase the detectability of selected variants of small effect, especially because local adaptation with gene flow can promote linkage disequilibrium around selected sites and aid their detection

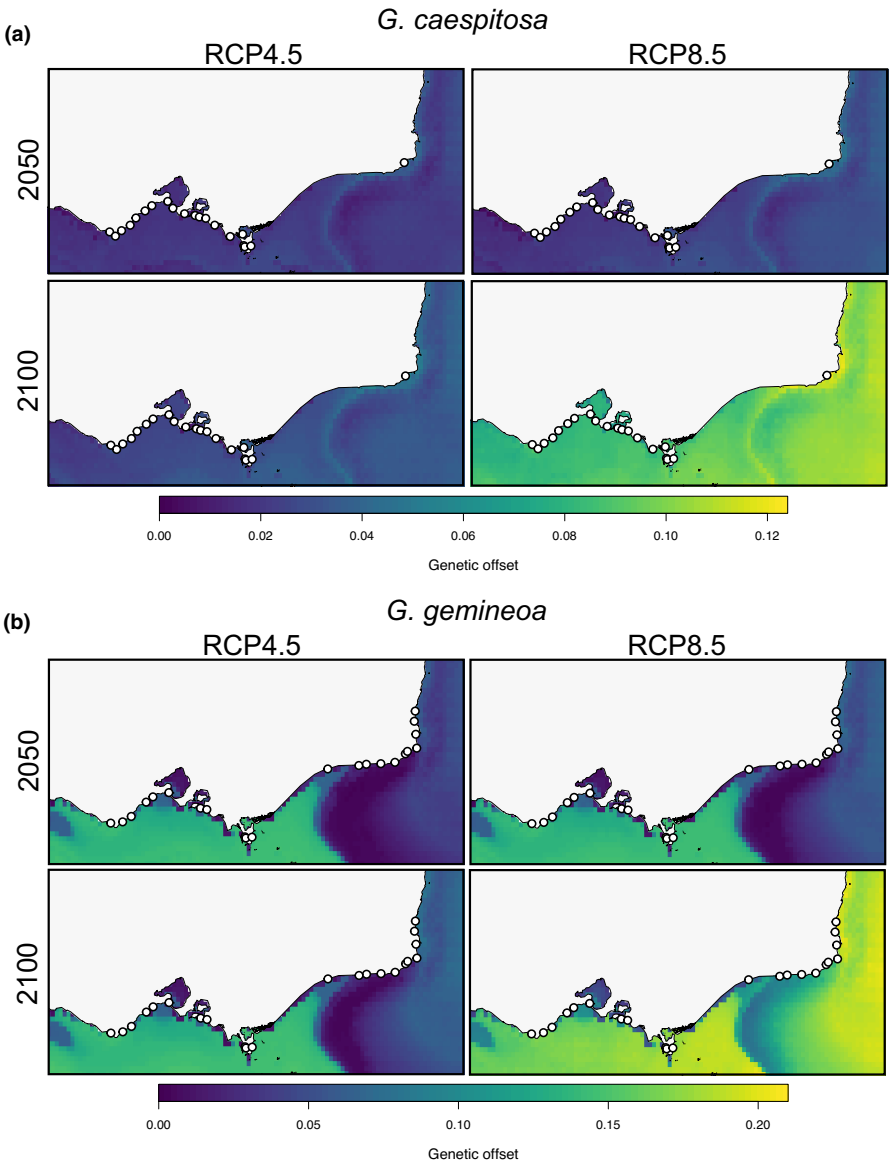

FIGURE 5 Genetic offsets predicted to maintain thermal adaptation under future climate change for (a) *Galeolaria caespitosa* and (b) *G. gemineoa* (note the differing scales). Predictions are shown for 2050 and 2100 under low (RCP4.5) and high (RCP8.5) CO_2 emission scenarios. Points are locations from which species were sampled. Species have planktonic life stages (gametes, embryos and larvae) that spend days to weeks offshore before transitioning to sessile stages (juveniles and adults) onshore in the intertidal zone.

with low-density markers (Charlesworth et al., 1997; Petry, 1983). Future work using denser markers, and model-based methods for exploring parallelism (e.g., Lee & Coop, 2017), would be important to inform hypotheses about modes of adaptation above.

Offsets from spatial modelling of allele frequencies at candidate loci predict that *G. gemineoa* is more genomically vulnerable than *G. caespitosa* to climate change, needing twice as much thermal adaptation in situ to maintain existing levels under projected warming (see caveats below). Since offsets rely on existing strengths of genotype–temperature associations (Fitzpatrick & Keller, 2015), this prediction probably reflects the stronger associations favoured by *G. gemineoa*'s wider latitudinal range compared to its sister species. Offsets also predict greater vulnerability for *G. caespitosa* on the northeast coast, which our data suggest is its northern range edge, and for *G. gemineoa* on the southwest coast, which is presumably its western range edge (although it may extend further west than we sampled). Compared to range cores, range-edge populations are predicted to be more evolutionarily dynamic, but also more prone to decline (Eckert et al., 2008; Polechová & Barton, 2015; Sexton et al., 2009). Our predictions could therefore point to the contraction or fragmentation of species' ranges in future climates, flagging range edges as priorities for validating predictions (e.g., through reciprocal transplants of core and edge populations; Hoffmann et al., 2021) and exploring the extent to which plasticity or future adaptation in situ might temper them. Last, offsets for *G. gemineoa* often predict lower vulnerability in bays than in adjacent coasts. Given our limited sampling in bays, however, more work is needed to clarify such patterns.

Despite their promise for identifying geographical regions where adaptation is predicted to be most vulnerable to disruption by climate change (Fitzpatrick et al., 2021), the tools used here have limitations worth acknowledging. First, as recent reviews (Capblancq et al., 2020; Hoffmann et al., 2021; Láruson et al., 2022; Rellstab et al., 2021) have emphasized, predictions of genomic vulnerability ignore the potential for plasticity, migration or future adaptation to buffer populations against climate change, and rely on genotype–environment associations whose links to phenotypes that

underpin adaptation require experimental validation. Since reduced-representation sequencing will also miss many of the loci involved in adaptation (Hoban et al., 2016; Hoffmann et al., 2021), supplementing data like ours with insights from quality reference genomes or whole-genome resequencing is a priority as such technologies become more accessible to nonmodel taxa. Second, remote sensing may adequately capture changes in coastal water temperatures over large spatial scales (Stobart et al., 2015), and on timescales relevant to climate adaptation (Rellstab et al., 2015), but poorly capture local extremes and variability (Lathlean et al., 2011; Riginos et al., 2016). The kind of satellite data used here remain standard for predicting genomic vulnerability in coastal species (e.g., Adam et al., 2022; Nielsen et al., 2021; Vranken et al., 2021; Wood et al., 2021), but targeted data from in situ loggers may be vital to tune or fill gaps in remote sensing. Moreover, while climate warming is considered a main driver of selection on such species (Penn & Deutsch, 2022), understanding its interplay with other potential drivers (e.g., water flow or chemistry) will also be important for refining predictions of genomic vulnerability to climate change in coastal ecosystems, especially as high-resolution time series become available.

Overall, we present parallel and nonparallel genomic signatures of climate adaptation for partly sympatric foundation species in a sentinel region for climate impacts. Insights into the repeatability of adaptation are rare for sister species such as *Galeolaria* (e.g., Hartke et al., 2021; see also Torrado et al., 2020), and are extended here by spatially explicit predictions of where disruption of adaptation could see species' ranges contract or fragment in future climates, and where experimental validation of predictions could be prioritized. Our results therefore identify sister *Galeolaria* species as evolutionarily significant units worth conserving for their genetic uniqueness and adaptive value (Foden et al., 2019; Smith et al., 2014; Willi et al., 2022), given the broader impacts of range shifts in foundation species on the biological communities they sustain (Thomsen et al., 2022). Further, we present genomic patterns of neutral variation suggesting that sister species are genetically isolated but adapting to local climates in spite of extensive gene flow across their ranges. Our work therefore has implications for understanding the genomic basis of adaptation and species barriers in the face of gene flow (e.g., Seehausen et al., 2014; Tigano & Friesen, 2016; Yeaman & Otto, 2011), and points to new opportunities to explore fundamental evolutionary hypotheses about its causes and consequences in warming coastal ecosystems.

AUTHOR CONTRIBUTIONS

All authors conceived and designed the study. C.G. carried out sampling and molecular laboratory work. C.G. carried out the bioinformatics and statistical analyses with significant input from K.H. and K.M. All authors significantly contributed to writing the manuscript.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Sequence data are available at the National Center for Biotechnology Information Sequence Read Archive (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA820542/). VCF files with filtered SNP data are available on Figshare (https://doi.org/10.6084/m9.figshare.21845031). Scripts and other input files are available on GitHub (https://github.com/CristobalGS/ClimateAdaptation-and-Vulnerability).

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REFERENCES

Adam, A. A. S., Thomas, L., Underwood, J., Gilmour, J., & Richards, Z. T. (2022). Population connectivity and genetic offset in the spawning coral *Acropora digitifera* in Western Australia. *Molecular Ecology*, *00*, 1–15. https://doi.org/10.1111/mec.16498

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*(9), 1655–1664. https://doi.org/10.1101/gr.094052.109

Andrews, K. R., Good, J. M., Miller, M. R., Luikart, G., & Hohenlohe, P. A. (2016). Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews. Genetics*, *17*(2), 81–92. https://doi.org/10.1038/nrg.2015.28

Ardura, A., Zaiko, A., Morán, P., Planes, S., & Garcia-Vazquez, E. (2017). Epigenetic signatures of invasive status in populations of marine invertebrates. *Scientific Reports*, *7*(1), 42193. https://doi.org/10.1038/srep42193

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & Clerck, O. D. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284. https://doi.org/10.1111/geb.12693

Barrett, R. D. H., & Schluter, D. (2008). Adaptation from standing genetic variation. *Trends in Ecology & Evolution*, *23*(1), 38–44. https://doi.org/10.1016/j.tree.2007.09.008

Bay, R. A., Harrigan, R. J., Underwood, V. L., Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*, *359*(6371), 83–86. https://doi.org/10.1126/science.aan4380

Bitter, M. C., Kapsenberg, L., Gattuso, J.-P., & Pfister, C. A. (2019). Standing genetic variation fuels rapid adaptation to ocean acidification. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-13767-1

Bitter, M. C., Wong, J. M., Dam, H. G., Donelan, S. C., Kenkel, C. D., Komoroske, L. M., Nickols, K. J., Rivest, E. B., Salinas, S., Burgess, S. C., & Lotterhos, K. E. (2021). Fluctuating selection and global change: A synthesis and review on disentangling the roles of climate amplitude, predictability and novelty. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1957), 20210727. https://doi.org/10.1098/rspb.2021.0727

Blount, Z. D., Lenski, R. E., & Losos, J. B. (2018). Contingency and determinism in evolution: Replaying life's tape. *Science*, *362*(6415), eaam5979. https://doi.org/10.1126/science.aam5979

Borrell, J. S., Zohren, J., Nichols, R. A., & Buggs, R. J. A. (2020). Genomic assessment of local adaptation in dwarf birch to inform assisted gene flow. *Evolutionary Applications*, *13*(1), 161–175. https://doi.org/10.1111/eva.12883

Capblancq, T., Fitzpatrick, M. C., Bay, R. A., Exposito-Alonso, M., & Keller, S. R. (2020). Genomic prediction of (mal)adaptation across current and future climatic landscapes. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 245–269. https://doi.org/10.1146/annurev-ecolsys-020720-042553

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, *22*(11), 3124–3140. https://doi.org/10.1111/mec.12354

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: Building and genotyping Loci de novo from short-read sequences. *G3 (Bethesda, Md.)*, *1*(3), 171–182. https://doi.org/10.1534/g3.111.000240

Charlesworth, B., Nordborg, M., & Charlesworth, D. (1997). The effects of local selection, balanced polymorphism and background selection on equilibrium patterns of genetic diversity in subdivided populations. *Genetics Research*, *70*(2), 155–174. https://doi.org/10.1017/S0016672397002954

Chirgwin, E., Connallon, T., & Monro, K. (2021). The thermal environment at fertilization mediates adaptive potential in the sea. *Evolution Letters*, *5*(2), 154–163. https://doi.org/10.1002/evl3.215

Chirgwin, E., Marshall, D. J., & Monro, K. (2020). Physical and physiological impacts of ocean warming alter phenotypic selection on sperm morphology. *Functional Ecology*, *34*(3), 646–657. https://doi.org/10.1111/1365-2435.13483

Cole, V. J., Hutchings, P. A., & Ross, P. M. (2018). Predicting biodiversity changes due to loss of bioengineers from an intertidal landscape, a case study from Sydney harbour. *Australian Zoologist*, *39*(2), 194–206. https://doi.org/10.7882/AZ.2015.034

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*, 65–70. https://doi.org/10.1126/science.aaz3658

Dawson, M. N. (2005). Incipient speciation of *Catostylus mosaicus* (Scyphozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in south-East Australia. *Journal of Biogeography*, *32*(3), 515–533. https://doi.org/10.1111/j.1365-2699.2004.01193.x

Eckert, C. G., Samis, K. E., & Lougheed, S. C. (2008). Genetic variation across species' geographical ranges: The central–marginal hypothesis and beyond. *Molecular Ecology*, *17*(5), 1170–1188. https://doi.org/10.1111/j.1365-294X.2007.03659.x

Ellis, N., Smith, S. J., & Pitcher, C. R. (2012). Gradient forests: Calculating importance gradients on physical predictors. *Ecology*, *93*(1), 156–168. https://doi.org/10.1890/11-0252.1

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fierst, J. L., & Hansen, T. F. (2010). Genetic architecture and postzygotic reproductive isolation: Evolution of Bateson–Dobzhansky–Muller incompatibilities in a polygenic model. *Evolution*, *64*(3), 675–693. https://doi.org/10.1111/j.1558-5646.2009.00861.x

Fischer, E. M., & Knutti, R. (2015). Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. *Nature Climate Change*, *5*(6), 560–564. https://doi.org/10.1038/nclimate2617

Fitzpatrick, M. C., Chhatre, V. E., Soolanayakanahally, R. Y., & Keller, S. R. (2021). Experimental support for genomic prediction of climate maladaptation using the machine learning approach gradient forests. *Molecular Ecology Resources*, *21*(8), 2749–2765. https://doi.org/10.1111/1755-0998.13374

Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, *18*(1), 1–16. https://doi.org/10.1111/ele.12376

Fitzpatrick, S. W., Bradburd, G. S., Kremer, C. T., Salerno, P. E., Angeloni, L. M., & Funk, W. C. (2020). Genomic and fitness consequences of genetic rescue in wild populations. *Current Biology*, *30*(3), 517–522. e5. https://doi.org/10.1016/j.cub.2019.11.062

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *WIREs Climate Change*, *10*(1), e551. https://doi.org/10.1002/wcc.551

Forester, B. R., Jones, M. R., Joost, S., Landguth, E. L., & Lasky, J. R. (2016). Detecting spatial genetic signatures of local adaptation in heterogeneous landscapes. *Molecular Ecology*, *25*(1), 104–120. https://doi.org/10.1111/mec.13476

Frankham, R. (2015). Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology*, *24*(11), 2610–2618. https://doi.org/10.1111/mec.13139

Gallegos, C., Hodgins, K. A., & Monro, K. (2022). *Climate adaptation and vulnerability of foundation species in a global change hotspot*. NCBI – SRA. Accession: PRJNA820542. [data set].

Galpern, P., Peres-Neto, P. R., Polfus, J., & Manseau, M. (2014). MEMGENE: Spatial pattern detection in genetic distance data. *Methods in Ecology and Evolution*, *5*(10), 1116–1120. https://doi.org/10.1111/2041-210X.12240

García-Ramos, G., & Kirkpatrick, M. (1997). Genetic models of adaptation and gene flow in peripheral populations. *Evolution*, *51*(1), 21–28. https://doi.org/10.1111/j.1558-5646.1997.tb02384.x

Gautier, M. (2015). Genome-wide scan for adaptive divergence and association with population-specific covariates. *Genetics*, *201*(4), 1555–1579. https://doi.org/10.1534/genetics.115.181453

Gaylord, B., & Gaines, S. D. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist*, *155*(6), 769–789. https://doi.org/10.1086/303357

Goudet, J., & Jombart, T. (2015). *hierfstat: Estimation and tests of hierarchical F-statistics* (R package version 0.04–22.). https://CRAN.R-project.org/package=hierfstat

Grant, P. R., & Grant, B. R. (2019). Hybridization increases population variation during adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(46), 23216–23224. https://doi.org/10.1073/pnas.1913534116

Grummer, J. A., Beheregaray, L. B., Bernatchez, L., Hand, B. K., Luikart, G., Narum, S. R., & Taylor, E. B. (2019). Aquatic landscape genomics and environmental effects on genetic variation. *Trends in Ecology and Evolution*, *34*(7), 641–654. https://doi.org/10.1016/j.tree.2019.02.013

Haldane, J. (1930). Theoretical genetics of autopolyploids. *Journal of Genetics*, *22*, 359–372.

Halt, M. N., Kupriyanova, E. K., Cooper, S. J. B., & Rouse, G. W. (2009). Naming species with no morphological indicators: Species status of *Galeolaria caespitosa* (Annelida: Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. *Invertebrate Systematics*, *23*(3), 205–222. https://doi.org/10.1071/IS09003

Hartke, J., Waldvogel, A.-M., Sprenger, P. P., Schmitt, T., Menzel, F., Pfenninger, M., & Feldmeyer, B. (2021). Little parallelism in genomic signatures of local adaptation in two sympatric, cryptic sister species. *Journal of Evolutionary Biology*, *34*(6), 937–952. https://doi.org/10.1111/jeb.13742

Hijmans, R. J. (2017). *Raster: Geographic data analysis and modeling*. https://CRAN.R-proje ct.org/package=raster

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hoban, S., Kelley, J. L., Lotterhos, K. E., Antolin, M. F., Bradburd, G., Lowry, D. B., Poss, M. L., Reed, L. K., Storfer, A., & Whitlock, M. C. (2016). Finding the genomic basis of local adaptation: Pitfalls, practical solutions, and future directions. *The American Naturalist*, *188*(4), 379–397. https://doi.org/10.1086/688018

Hobday, A. J., & Lough, J. M. (2011). Projected climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, *62*, 1000–1014.

Hobday, A. J., & Pecl, G. T. (2014). Identification of global marine hotspots: Sentinels for change and vanguards for adaptation action. *Reviews in Fish Biology and Fisheries*, *24*(2), 415–425. https://doi.org/10.1007/s11160-013-9326-6

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Hoffmann, A. A., Weeks, A. R., & Sgrò, C. M. (2021). Opportunities and challenges in assessing climate change vulnerability through genomics. *Cell*, *184*(6), 1420–1425. https://doi.org/10.1016/j.cell.2021.02.006

Hohenlohe, P. A., Funk, W. C., & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Molecular Ecology*, *30*(1), 62–82. https://doi.org/10.1111/mec.15720

Howard, D. J. (1999). Conspecific sperm and pollen precedence and speciation. *Annual Review of Ecology and Systematics*, *30*(1), 109–132. https://doi.org/10.1146/annurev.ecolsys.30.1.109

Ingvarsson, P. K., & Bernhardsson, C. (2020). Genome-wide signatures of environmental adaptation in European aspen (*Populus tremula*) under current and future climate conditions. *Evolutionary Applications*, *13*(1), 132–142. https://doi.org/10.1111/eva.12792

Jia, K.-H., Zhao, W., Maier, P. A., Hu, X.-G., Jin, Y., Zhou, S.-S., Jiao, S.-Q., El-Kassaby, Y. A., Wang, T., Wang, X.-R., & Mao, J.-F. (2020). Landscape genomics predicts climate change-related genetic offset for the widespread *Platycladus orientalis* (Cupressaceae). *Evolutionary Applications*, *13*(4), 665–676. https://doi.org/10.1111/eva.12891

Jombart, T. (2008). Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*(11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kardos, M., Armstrong, E. E., Fitzpatrick, S. W., Hauser, S., Hedrick, P. W., Miller, J. M., Tallmon, D. A., & Funk, W. C. (2021). The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(48), e2104642118. https://doi.org/10.1073/pnas.2104642118

Kingsolver, J. G., & Buckley, L. B. (2017). Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160147. https://doi.org/10.1098/rstb.2016.0147

Knaus, B. J., & Grünwald, N. J. (2017). Vcfr: A package to manipulate and visualize variant call format data in R. *Molecular Ecology Resources*, *17*(1), 44–53. https://doi.org/10.1111/1755-0998.12549

Lande, R. (2014). Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. *Journal of Evolutionary Biology*, *27*(5), 866–875. https://doi.org/10.1111/jeb.12360

Láruson, Á. J., Fitzpatrick, M. C., Keller, S. R., Haller, B. C., & Lotterhos, K. E. (2022). Seeing the forest for the trees: Assessing genetic offset predictions from gradient forest. *Evolutionary Applications*, *15*(3), 403–416. https://doi.org/10.1111/eva.13354

Lathlean, J. A., Ayre, D. J., & Minchinton, T. E. (2011). Rocky intertidal temperature variability along the southeast coast of Australia: Comparing data from in situ loggers, satellite-derived SST and terrestrial weather stations. *Marine Ecology Progress Series*, *439*(May), 83–95. https://doi.org/10.3354/meps09317

Lee, K. M., & Coop, G. (2017). Distinguishing among modes of convergent adaptation using population genomic data. *Genetics*, *207*(4), 1591–1619. https://doi.org/10.1534/genetics.117.300417

Legendre, P., & Fortin, M.-J. (2010). Comparison of the mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources*, *10*(5), 831–844. https://doi.org/10.1111/j.1755-0998.2010.02866.x

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*, *17*(4), 183–189. https://doi.org/10.1016/S0169-5347(02)02497-7

Lenormand, T., Chevin, L.-M., & Bataillon, T. (2016). Parallel evolution: What does it (not) tell us and why is it (still) interesting? In G. Ramsey & C. H. Pence (Eds.), *Chance in evolution* (pp. 96–222). University of Chicago Press. https://doi.org/10.7208/chicago/9780226401911.003.0009

Liggins, L., Treml, E. A., & Riginos, C. (2019). Seascape genomics: Contextualizing adaptive and neutral genomic variation in the ocean environment. In *Population genomics: Marine organisms* (pp. 171–218). Springer. https://doi.org/10.1007/13836_2019_68

Lotterhos, K. E., Albecker, M., & Trussell, G. C. (2021). Evolution in changing seas. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1965), 20212443. https://doi.org/10.1098/rspb.2021.2443

Lotterhos, K. E., & Levitan, D. R. (2010). Gamete release and spawning behavior in broadcast spawning marine invertebrates. In J. L. Leonard & A. Córdoba-Aguilar (Eds.), *The evolution of primary sexual characters in animals* (pp. 99–120). Oxford University Press.

Miller, A. D., Coleman, M. A., Clark, J., Cook, R., Naga, Z., Doblin, M. A., Hoffmann, A. A., Sherman, C. D. H., & Bellgrove, A. (2020). Local thermal adaptation and limited gene flow constrain future climate responses of a marine ecosystem engineer. *Evolutionary Applications*, *13*(5), 918–934. https://doi.org/10.1111/eva.12909

Mitchell, N., Owens, G. L., Hovick, S. M., Rieseberg, L. H., & Whitney, K. D. (2019). Hybridization speeds adaptive evolution in an eight-year field experiment. *Scientific Reports*, *9*(1), 6746. https://doi.org/10.1038/s41598-019-43119-4

Nazareno, A. G., Bemmels, J. B., Dick, C. W., & Lohmann, L. G. (2017). Minimum sample sizes for population genomics: An empirical study from an Amazonian plant species. *Molecular Ecology Resources*, *17*(6), 1136–1147. https://doi.org/10.1111/1755-0998.12654

Nielsen, E. S., Henriques, R., Beger, M., & von der Heyden, S. (2021). Distinct interspecific and intraspecific vulnerability of coastal species to global change. *Global Change Biology*, *27*(15), 3415–3431. https://doi.org/10.1111/gcb.15651

O'Hara, T. D., & Poore, G. C. B. (2000). Patterns of distribution for southern Australian marine echinoderms and decapods. *Journal of Biogeography*, *27*, 1321–1335. https://doi.org/10.1046/j.1365-2699.2000.00499.x

Olsen, K. C., Ryan, W. H., Winn, A. A., Kosman, E. T., Moscoso, J. A., Krueger-Hadfield, S. A., Burgess, S. C., Carlon, D. B., Grosberg, R. K., Kalisz, S., & Levitan, D. R. (2020). Inbreeding shapes the evolution of marine invertebrates. *Evolution*, *74*(5), 871–882. https://doi.org/10.1111/evo.13951

Paris, J. R., Stevens, J. R., & Catchen, J. M. (2017). Lost in parameter space: A road map for stacks. *Methods in Ecology and Evolution*, *8*(10), 1360–1373. https://doi.org/10.1111/2041-210X.12775

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214. https://doi.org/10.1126/science.aai9214

Penn, J. L., & Deutsch, C. (2022). Avoiding ocean mass extinction from climate warming. *Science*, *376*(6592), 524–526. https://doi.org/10.1126/science.abe9039

Perdry, H., & Dandine-Roulland, C. (2020). *gaston: Genetic data handling (QC, GRM, LD, PCA) & linear mixed models. (R package version 1.5.6.)*. https://CRAN.R-project.org/package=gaston

Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One*, *7*(5), e37135. https://doi.org/10.1371/journal.pone.0037135

Petry, D. (1983). The effect on neutral gene flow of selection at a linked locus. *Theoretical Population Biology*, *23*(3), 300–313. https://doi.org/10.1016/0040-5809(83)90020-5

Pina-Martins, F., Baptista, J., Pappas, G., & Paulo, O. S. (2019). New insights into adaptation and population structure of cork oak using genotyping by sequencing. *Global Change Biology*, *25*(1), 337–350. https://doi.org/10.1111/gcb.14497

Pinsky, M. L., & Fredston, A. (2022). A stark future for ocean life. *Science*, *376*(6592), 452–453. https://doi.org/10.1126/science.abo4259

Plough, L. V. (2016). Genetic load in marine animals: A review. *Current Zoology*, *62*(6), 567–579. https://doi.org/10.1093/cz/zow096

Poland, J. A., Brown, P. J., Sorrells, M. E., & Jannink, J. L. (2012). Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. *PLoS One*, *7*(2), e32253. https://doi.org/10.1371/journal.pone.0032253

Polechová, J. (2018). Is the sky the limit? On the expansion threshold of a species' range. *PLoS Biology*, *16*(6), 1–18. https://doi.org/10.1371/journal.pbio.2005372

Polechová, J., & Barton, N. H. (2015). Limits to adaptation along environmental gradients. *Proceedings of the National Academy of Sciences*, *112*(20), 6401–6406. https://doi.org/10.1073/pnas.1421515112

Pootakham, W., Sonthirod, C., Naktang, C., Jomchai, N., Sangsrakru, D., & Tangphatsornruang, S. (2016). Effects of methylation-sensitive enzymes on the enrichment of genic SNPs and the degree of genome complexity reduction in a two-enzyme genotyping-by-sequencing (GBS) approach: A case study in oil palm (Elaeis guineensis). *Molecular Breeding*, *36*(11), 154. https://doi.org/10.1007/s11032-016-0572-x

Qiagen. (2006). *DNeasy blood & tissue handbook*.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.R-project.org/

Ramírez, F., Afán, I., Davis, L. S., & Chiaradia, A. (2017). Climate impacts on global hot spots of marine biodiversity. *Science Advances*, *3*(2), e1601198. https://doi.org/10.1126/sciadv.1601198

Rautsaw, R. M., Schramer, T. D., Acuña, R., Arick, L. N., DiMeo, M., Mercier, K. P., Schrum, M., Mason, A. J., Margres, M. J., Strickland, J. L., & Parkinson, C. L. (2021). Genomic adaptations to salinity resist gene flow in the evolution of floridian watersnakes. *Molecular Biology and Evolution*, *38*(3), 745–760. https://doi.org/10.1093/molbev/msaa266

Rebolledo, A. P., Sgrò, C. M., & Monro, K. (2020). Thermal performance curves reveal shifts in optima, limits and breadth in early life. *Journal of Experimental Biology*, *223*(22), jeb233254. https://doi.org/10.1242/jeb.233254

Reed, D. H., & Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conservation Biology*, *17*(1), 230–237. https://doi.org/10.1046/j.1523-1739.2003.01236.x

Rellstab, C., Dauphin, B., & Exposito-Alonso, M. (2021). Prospects and limitations of genomic offset in conservation management. *Evolutionary Applications*, *14*(5), 1202–1212. https://doi.org/10.1111/eva.13205

Rellstab, C., Gugerli, F., Eckert, A. J., Hancock, A. M., & Holderegger, R. (2015). A practical guide to environmental association analysis in landscape genomics. *Molecular Ecology*, *24*(17), 4348–4370. https://doi.org/10.1111/mec.13322

Rescan, M., Grulois, D., Aboud, E. O., de Villemereuil, P., & Chevin, L.-M. (2021). Predicting population genetic change in an autocorrelated random environment: Insights from a large automated experiment. *PLoS Genetics*, *17*(6), e1009611. https://doi.org/10.1371/journal.pgen.1009611

Ridgway, K., & Hill, K. (2009). The east Australian current. In E. S. Poloczanska, A. J. Hobday, & A. J. Richardson (Eds.), *A marine climate change impacts and adaptation report card for Australia 2009* (p. 17). NCCARF Publication.

Ridgway, K. R. (2007). Seasonal circulation around Tasmania: An interface between eastern and western boundary dynamics. *Journal of Geophysical Research: Oceans*, *112*(C10). https://doi.org/10.1029/2006JC003898

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: How spatial analyses can augment population genomic studies. *Current Zoology*, *62*(6), 581–601. https://doi.org/10.1093/cz/zow067

Ripa, J., & Lundberg, P. (1996). Noise colour and the risk of population extinctions. *Proceedings of the Royal Society B: Biological Sciences*, *263*(1377), 1751–1753. https://doi.org/10.1098/rspb.1996.0256

Rochette, N. C., & Catchen, J. M. (2017). Deriving genotypes from RAD-seq short-read data using stacks. *Nature Protocols*, *12*(12), 2640–2659. https://doi.org/10.1038/nprot.2017.123

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(8), 4211–4217. https://doi.org/10.1073/pnas.1913007117

Ruokolainen, L., Lindén, A., Kaitala, V., & Fowler, M. S. (2009). Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology and Evolution*, *24*(10), 555–563. https://doi.org/10.1016/j.tree.2009.04.009

Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation. *Nature Reviews Genetics*, *14*(11), 807–820. https://doi.org/10.1038/nrg3522

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313), 719. https://doi.org/10.1126/science.aaf7671

Seehausen, O., Butlin, R. K., Keller, I., Wagner, C. E., Boughman, J. W., Hohenlohe, P. A., Peichel, C. L., Saetre, G. P., Bank, C., Brännström, A., Brelsford, A., Clarkson, C. S., Eroukhmanoff, F., Feder, J. L., Fischer, M. C., Foote, A. D., Foote, A. D., Franchini, P., Jiggins, C. D., … Widmer, A. (2014). Genomics and the origin of species. *Nature Reviews Genetics*, *15*(3), 176–192. https://doi.org/10.1038/nrg3644

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sgrò, C. M., Lowe, A. J., & Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, *4*(2), 326–337. https://doi.org/10.1111/j.1752-4571.2010.00157.x

Sinervo, B., & Calsbeek, R. (2003). Physiological epistasis, ontogenetic conflict and natural selection on physiology and life history. *Integrative and Comparative Biology*, *43*(3), 419–430. https://doi.org/10.1093/icb/43.3.419

Smith, T. B., Kinnison, M. T., Strauss, S. Y., Fuller, T. L., & Carroll, S. P. (2014). Prescriptive evolution to conserve and manage biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 1–22. https://doi.org/10.1146/annurev-ecolsys-120213-091747

Stern, D. L. (2013). The genetic causes of convergent evolution. *Nature Reviews Genetics*, *14*, 751–764. https://doi.org/10.1038/nrg3483

Stobart, B., Mayfield, S., Mundy, C., Hobday, A. J., Hartog, J. R., Stobart, B., Mayfield, S., Mundy, C., Hobday, A. J., & Hartog, J. R. (2015). Comparison of in situ and satellite sea surface-temperature data from South Australia and Tasmania: How reliable are satellite data as a proxy for coastal temperatures in temperate southern Australia? *Marine and Freshwater Research*, *67*(5), 612–625. https://doi.org/10.1071/MF14340

Strathmann, R. R. (1990). Why life histories evolve differently in the sea. *American Zoologist*, *30*(1), 197–207. https://doi.org/10.1093/icb/30.1.197

Styan, C. A., Kupriyanova, E., & Havenhand, J. N. (2008). Barriers to cross-fertilization between populations of a widely dispersed polychaete species are unlikely to have arisen through gametic compatibility arms-races. *Evolution*, *62*(12), 3041–3055. https://doi.org/10.1111/j.1558-5646.2008.00521.x

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*(9), 944–953. https://doi.org/10.1111/ele.12474

Teixeira, J. C., & Huber, C. D. (2021). The inflated significance of neutral genetic diversity in conservation genetics. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(10), e201509611. https://doi.org/10.1073/pnas.2015096118

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Bulleri, F., Farhan, R., Frühling, V. M. M., Gribben, P. E., Harrison, S. B., He, Q., Klinghardt, M., Langeneck, J., Lanham, B. S., Mondardini, L., Mulders, Y., Oleksyn, S., Ramus, A. P., Schiel, D. R., Schneider, T., … Zotz, G. (2022). Heterogeneity within and among co-occurring foundation species increases biodiversity. *Nature Communications*, *13*(1), 581. https://doi.org/10.1038/s41467-022-28194-y

Tigano, A., & Friesen, V. L. (2016). Genomics of local adaptation with gene flow. *Molecular Ecology*, *25*(10), 2144–2164. https://doi.org/10.1111/mec.13606

Todesco, M., Pascual, M. A., Owens, G. L., Ostevik, K. L., Moyers, B. T., Hübner, S., Heredia, S. M., Hahn, M. A., Caseys, C., Bock, D. G., & Rieseberg, L. H. (2016). Hybridization and extinction. *Evolutionary Applications*, *9*(7), 892–908. https://doi.org/10.1111/eva.12367

Torrado, H., Carreras, C., Raventos, N., Macpherson, E., & Pascual, M. (2020). Individual-based population genomics reveal different drivers of adaptation in sympatric fish. *Scientific Reports*, *10*(1), 12683. https://doi.org/10.1038/s41598-020-69160-2

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & Clerck, O. D. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

Vranken, S., Wernberg, T., Scheben, A., Severn-Ellis, A. A., Batley, J., Bayer, P. E., Edwards, D., Wheeler, D., & Coleman, M. A. (2021). Genotype–environment mismatch of kelp forests under climate change. *Molecular Ecology*, *30*(15), 3730–3746. https://doi.org/10.1111/mec.15993

Waldock, C., Dornelas, M., & Bates, A. E. (2018). Temperature-driven biodiversity change: Disentangling space and time. *Bioscience*, *68*(11), 873–884. https://doi.org/10.1093/biosci/biy096

Waters, J. M. (2008). Marine biogeographical disjunction in temperate Australia: Historical landbridge, contemporary currents, or both? *Diversity and Distributions*, *14*(4), 692–700. https://doi.org/10.1111/j.1472-4642.2008.00481.x

Willi, Y., Kristensen, T. N., Sgrò, C. M., Weeks, A. R., Ørsted, M., & Hoffmann, A. A. (2022). Conservation genetics as a management tool: The five best-supported paradigms to assist the management of threatened species. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(1), e2105076119. https://doi.org/10.1073/pnas.2105076119

Wood, G., Marzinelli, E. M., Campbell, A. H., Steinberg, P. D., Vergés, A., & Coleman, M. A. (2021). Genomic vulnerability of a dominant seaweed points to future-proofing pathways for Australia's underwater forests. *Global Change Biology*, *27*(10), 2200–2212. https://doi.org/10.1111/gcb.15534

Wood, T. E., Burke, J. M., & Rieseberg, L. H. (2005). Parallel genotypic adaptation: When evolution repeats itself. In R. Mauricio (Ed.), *Genetics of adaptation* (pp. 157–170). Springer. https://doi.org/10.1007/1-4020-3836-4_14

Wright, J. T., & Gribben, P. E. (2017). Disturbance-mediated facilitation by an intertidal ecosystem engineer. *Ecology*, *98*(9), 2425–2436. https://doi.org/10.1002/ecy.1932

Yeaman, S., Hodgins, K. A., Lotterhos, K. E., Suren, H., Nadeau, S., Degner, J. C., Nurkowski, K. A., Smets, P., Wang, T., Gray, L. K., Liepe, K. J., Hamann, A., Holliday, J. A., Whitlock, M. C., Rieseberg, L. H., & Aitken, S. N. (2016). Convergent local adaptation to climate in distantly related conifers. *Science*, *353*(6306), 1431–1433.

Yeaman, S., & Otto, S. P. (2011). Establishment and maintenance of adaptive genetic divergence under migration, selection, and drift. *Evolution*, *65*(7), 2123–2129. https://doi.org/10.1111/j.1558-5646.2011.01277.x

Yeaman, S., & Whitlock, M. C. (2011). The genetic architecture of adaptation under migration–selection balance. *Evolution*, *65*(7), 1897–1911. doi:10.1111/j.1558-5646.2011.01269.x

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