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Long-Term Stability of Marine Forests Facing Moderate Gradual Warming in a Remote Biodiversity Hotspot

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ABSTRACT

Aim: Ocean warming and marine heatwaves are rapidly reconfiguring the composition of seaweed forests—the world's largest coastal vegetated biome. Seaweed forest responses to climate change in remote locations, which constitute the majority of the forest biome, remain however poorly quantified. Here, we examine the temporal stability of the seaweed forests across a global seaweed biodiversity hotspot where several species are predicted to undergo severe range contractions in this century.

Location: Western south coast of Australia.

Methods: Seaweed forest canopies were censused at 18 shallow (<10 m) sheltered reefs between 1997 and 2006 and again between 2021 and 2024 (six sites per location). We also surveyed 24 sites to examine whether temporal changes differed over gradients of wave exposure and depth.

Results: Seaweed forest canopies across all locations showed surprisingly little change in biomass, cover, stand density and species composition over two decades, with strong spatial structuring across depth and exposure gradients persisting over time. The average thermal affinity of forest canopies (i.e., the community temperature index, CTI) did not track warming, suggesting that factors other than temperature (e.g., wave exposure and depth) are more important drivers of forest stand structure and/or that key thermal thresholds have not yet been crossed. Forests in the location with the most pronounced warming exhibited increased thermal bias over time (total bias of 0.8°C–2.2°C), indicating they were dominated by species with cooler affinities than their local temperatures.

Main Conclusions: The greater thermal bias in forests at the warmer edge of southern Australia suggests these will be more susceptible to future warming-related compositional changes than forests in cooler locations. The relative stability we found contrasts with a current context of rapidly changing seaweed forests nationally and globally, highlighting the need to deepen our ecological understanding of the region so that future changes to its unique biodiversity and ecosystem services can be predicted and mitigated.

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1 | Introduction

Earth's ecosystems are being transformed by anthropogenic pressures acting at increasingly larger spatial scales, with global climate change emerging as the dominant driver of change in many ecosystems (Halpern et al. 2019; IPCC 2023). As a result, our understanding of ecosystem change and corresponding conservation decisions increasingly relies on maps and assessments conducted at large spatial scales (i.e., global and continental scales; UNEP 2023). Global synthesis and maps are extremely useful to identify particularly vulnerable species or locations, and for helping to prioritise global conservation efforts (Brooks et al. 2006). Yet, responses to climate change are often species and location specific (IPCC 2023), and it is increasingly recognised that our understanding of change and ecosystem vulnerability is limited by data typically being clustered around populated areas which receive disproportionate research focus (Feeley, Stroud, and Perez 2017; Meyer and Pebesma 2022). These data, however, may not necessarily reflect the trends, drivers of change and ecosystem characteristics of remote, less populated areas, leading to discrepancies between regional and global assessments or predictions (Ploton et al. 2020). Producing a comprehensive understanding of how climate change is affecting the Earth's natural systems thus requires a conscious effort to study more remote ecosystems as well as reporting and publishing non-significant results (Feeley, Stroud, and Perez 2017).

There is increased recognition that the responses of ecosystems, species and populations to climate change are often highly spatially variable, leading to a heterogeneity in outcomes at regional and local scales (Helmuth et al. 2014; Starko et al. 2024). This is particularly true for marine environments, where small differences in depth and wave exposure often create microclimates in locations separated by just a few metres, which can drastically affect the vulnerability of species and ecosystems to climate change (Grimaldi et al. 2023; Starko et al. 2022). For instance, at the community level, studies have documented change following marine heatwaves to be greater on the leeward sides of islands, which generally experience lower water turnover and warmer conditions than windward sides, where temperatures are typically cooler and less variable (Obura and Mangubhai 2011; McClanahan and Muthiga 2021). Shallow communities can also be more sensitive to temperature changes than deeper communities due to higher thermal exposure (Arriaga et al. 2024; Giraldo-Ospina, Kendrick, and Hovey 2020), which results in the migration of shallow mobile species to greater depths (Dulvy et al. 2008). Besides environmental microclimates, species environmental filtering and genetic adaptation can also vary across short spatial scales, strongly mediating biological responses to climate change (Starko et al. 2024). Integrating fine-scale variation in environmental conditions into climate impact assessments is therefore needed to improve the interpretation and prediction of responses to climate change, as well as identifying climatic refuges for temperature-sensitive species.

Forests of large brown seaweeds—typically kelps (order Laminariales) and fucoids (order Fucales)—form one of the most extensive coastal biomes on the planet which provides immense ecological and economic values every year (Duarte et al. 2022; Eger et al. 2023). Seaweed forests in temperate regions are undergoing rapid transformation under climate change, with marine heatwaves driving local extirpations (Krumhansl et al. 2016; Smale 2019; Wernberg, Krumhansl, et al. 2019), and warm-affinity species (tropical and warm-temperate species, sensu Lüning 1990) becoming more abundant at the expense of cold-affinity ones (Arriaga et al. 2024; Pessarrodona, Foggo, and Smale 2018; Soler et al. 2022; but see Gallon et al. 2014). Canopy-forming species are particularly vulnerable to warming and marine heatwaves because their biogeographic ranges are often directly determined by temperature (Lüning 1990), and their relatively limited dispersal capacity (Dayton 1973; Durrant et al. 2014) prevents them from tracking the speed of warming (Wood et al. 2021). Knowledge of the responses of seaweed forests to climate change is strongly spatially clustered along populated coastlines (e.g., Europe, the US, eastern Australia, Krumhansl et al. 2016; Smale 2019), despite the largest extent of the seaweed forest biome being in remote regions (Jayathilake and Costello 2021; UNEP 2023). Advances in remote sensing have revolutionised the monitoring of surface-floating seaweed forests in isolated areas (Mora-Soto et al. 2021), but a large fraction of the forest biome in remote areas is composed of non-surface-floating species which cannot be presently remotely sensed (e.g., forests in Southern Australia, Northern Canada and Russia), and whose response to climate change remains more poorly quantified.

Some of the most unique, extensive, and biodiverse seaweed forests on the planet are found in the waters of temperate Australia, which contain ~15% of the world's seaweed species (Phillips 2001). These forests are the biological engine of shallow Australian temperate reefs, fuelling food webs, carbon export to the deep sea, and providing habitat and refuge for a myriad of endemic species (Bennett et al. 2016; van der Mheen et al. 2024). Temperate Australian seaweed forests are a global biodiversity hotspot (Fragkopoulou et al. 2022; > 60 species of canopy forming species) and harbour millions of years of evolutionary history as 50% of global forest-forming seaweed families occur in that area (Guiry and Guiry 2022). Despite this staggering diversity, most research on the response of seaweed forests to climate change in this globally significant region has focused on kelp forest canopies (Butler et al. 2020; Connell et al. 2008; Vergés et al. 2016; Wernberg et al. 2016)—particularly those of *Ecklonia radiata* (Wernberg, Coleman, et al. 2019). This species dominates along the eastern and western coasts of Australia, where canopies are often monospecific. In contrast, comparatively less is known about the more speciose forest canopies along the longer—more remote—southern coast. Here, a diverse mix of poorly studied endemic fucoids dominate the canopies of moderately exposed and sheltered reefs (+14 species co-occurring in the same canopy; Collings 1996; Pessarrodona and Grimaldi 2022; Wernberg, Kendrick, and Phillips 2003). Southern Australian forests are composed by a mix of species of different thermal affinities, including a tropical element, a warm-temperate element and a cold-temperate element (Phillips 2001). In response to projected end-of-century warming, severe declines and local extinctions (36%–100% of range loss) are predicted for the cold-temperate species, particularly along the south-western corner of Australia, which constitutes the warm range edge of several endemic species (Martínez et al. 2018). In contrast, warmer affinity species are expected to be less severely affected or may even benefit (Martínez et al. 2018), potentially leading them to play increasingly important roles in future community structuring and ecosystem functioning. Whether this expected climate-driven forest reconfiguration is occurring remains, however, largely unknown.

The community temperature index (CTI) is a useful measure to track the effects of warming on species dominance and community composition, as it is a community-wide average of species' thermal affinities in a given location. The fact that seaweed biogeographical distributions often reflect their thermal ranges (Breeman 1990) makes the CTI a particularly powerful indicator of community response to warming and marine heatwaves (Burrows et al. 2020; Soler et al. 2022). An increasing CTI in response to warming can be associated with declines in cold-affinity species (Tayleur et al. 2016), increases in warm-affinity species (de Azevedo et al. 2023) or both (Arriaga et al. 2024).

Here, we examine forest canopies across three different locations and microhabitats (36 sites in total) in a remote area of southern Australia (Figure 1A) over a period of two decades characterised by rising water temperatures (Figure 1B–E). We hypothesise that:

i. Seaweed forest communities in shallow sheltered reefs will have changed over the past two decades, with changes being greatest westwards (Hamelin Bay, C), which has experienced an intense marine heatwave (Figure 1B) and greater warming in general (Figure 1C–E).
ii. Community changes will have been greater in reefs situated in shallow sheltered microclimates than reefs in exposed and deeper microclimates.
iii. Community changes over the past two decades will reflect species' biogeographical affinities, with warm-affinity species increasing at the expense of cold-affinity ones.

2 | Methods

2.1 | Study Areas and Design

The western south coast of Australia is located within a dry climate with little nutrient input from seasonally dry rivers and an eastward flowing surface current that depresses upwelling onto the shelf, resulting in a nutrient-poor oceanographic setting (0.01–0.13 μM nitrate year-round; McCosker, Davies, and Beckley 2020). Primary production is dominated by benthic producers and nutrient inputs are rapidly depleted following pulse accumulations (Lourey and Kirkman 2009). The study locations (Hamelin Bay, Bremer Bay, and Esperance Bay, Figure 1C–E) are situated offshore (1–13 km) of scarcely populated areas with some livestock pasture, where agricultural activities do not constitute important sources of nitrogen to the coastal system (Gorman, Russell, and Connell 2009). All locations lie within a microtidal regime at a similar latitude and are bathed by an extension of the poleward-flowing Leeuwin current. The Leeuwin

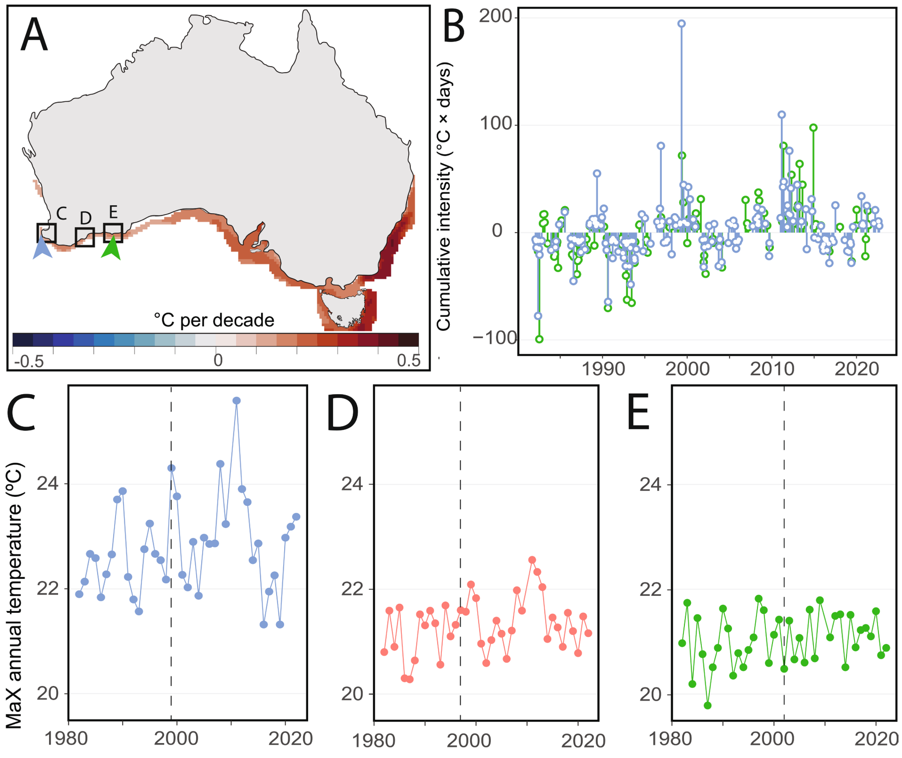

FIGURE 1 | Study locations across Southwest Australia and sea temperature change. (A) Coastal sea surface temperature trends (°C per decade, 1992–2023) within the temperate waters of southern Australia. Cells with no significant trend and warming in tropical coastlines are not shown. (B) Cumulative intensity of marine heatwaves (positive values; sensu (Schlegel et al. 2017)) and marine cold-spells (negative values) at our study locations: Hamelin Bay, depicted in blue, and blue arrow in (A); and Esperance Bay, depicted in green, and green arrow in (A). Cumulative intensity (i.e., the sum of daily intensities) is an indication of the total amount of heat or cold experienced. Maximum monthly annual sea surface temperature trends within the study locations of Hamelin (C), Bremer (D) and Esperance (E) Bay. The dotted line shows the year of historical sampling. Data were acquired from the NOAA OISST v2.1 data set.

transports warm, nutrient-poor water eastward over the shelf (Hamelin to Bremer Bay), its influence progressively waning as it moves offshore near the shelf break along Esperance (Kendrick et al. 2009). In general, the Leeuwin impedes upwelling of cold, nutrient-rich water from below the outer shelf edge. Biogeographically, the study locations lie within a transition zone between the kelp-dominated west Australian coast and the fucoid (*Cystophora* and *Sargassum* spp.) dominated south coast (Goldberg and Kendrick 2004; Wernberg, Coleman, et al. 2019; Wernberg, Kendrick, and Phillips 2003). Forest species composition varies across wave exposures (Goldberg and Kendrick 2004; Pessarrodona and Grimaldi 2022; Shepherd and Womersley 1981; Wernberg and Connell 2008) but with often no single dominant species (Turner and Cheshire 2003).

2.2 | Change in Shallow Sheltered Reefs

We repeated historical surveys of canopy-forming seaweeds in shallow (< 10 m in depth), relatively sheltered reefs across 700 km of coastline in southern Australia (Table 1). At all sites, we followed historical sampling methodologies (see extended methodology in the Data S1 for a detailed description of the sampling sites and protocols), which involved measuring the abundance (percent cover or biomass) of canopy-forming and understorey species within 50 × 50 cm (0.25 m^2) quadrats. We relocated the original sites using GPS coordinates, maps, and conversations with the original surveyors. Our shallow reef surveys focused on three locations with six sites nested within each location ($n = 18$, Table 1), with sites being relatively sheltered from the prevailing swell by submerged reefs or coastal features. Fishing was allowed at all the sites surveyed except for Cosy Corner and Cosy Corner 2 in Hamelin Bay, where fishing has been banned since 2012. At each site, macroalgae > 1 cm in length within each quadrat were counted in situ or harvested by hand and collected within calico bags, which were then sorted to species and wet weighed after removing excess water by shaking. Canopy-forming macroalgae (species in the orders Fucales and Laminariales) were then sorted to species and into the following groups: *Ecklonia radiata*; *Scytothalia dorycarpa*; *Cystophora* spp.; Sargassum *sensu lato* spp. (hereafter *Sargassum* spp.), which included species in the genus *Sargassum*, *Phyllotricha* and *Sargassopsis*; and other canopy-forming algae (*Scaberia*, *Acrocarpia*, *Platythalia*, *Caulocystis*). These groups reflect morphofunctional differences in canopy structural complexity, canopy effects on the surrounding environment and canopy species phenology, reproductive strategy and wave tolerance (Irving and Connell 2006; Pessarrodona and Grimaldi 2022). We focused on canopy-forming species as they are the principal ecosystem engineers of the forest (Pessarrodona and Grimaldi 2022), grouping non-canopy forming algae into an ‘understorey and epiphytes’ category.

2.3 | Change Across Depth and Wave Exposure

To examine change at local spatial scales (10s–100s of metres), we sampled reefs following historical protocols along gradients of depth (< 10 m and 10–20 m) and wave exposure in Esperance Bay. Exposed sites faced the Southern Ocean's predominant south-westerly swell, while sheltered sites were located on the leeward side of islands. We sampled six quadrats at six sites in each treatment, yielding a total of 144 samples (quadrats).

2.4 | Changes in Community Thermal Affinity

To establish whether changes in species abundance were related to their thermal affinity, and whether the community's thermal affinity tracked warming trends, we examined temporal changes in the community temperature index (CTI). CTI is the abundance-weighted average of species thermal affinities, which are calculated from each species temperature index (STI)—the thermal mid-point of a species' realised thermal distribution. The STI is a good proxy for seaweed thermal affinity as maximum incidence of species often occurs at the centre of their realised thermal range (Figure S1). The responsiveness of the CTI to temperature change can be predicted by the variation of thermal affinities among forest species (community thermal diversity, CTDiv)—calculated as the abundance-weighted standard deviation of STIs; and the community thermal range (CTR)—calculated as the abundance-weighted average width of species' thermal ranges (STRs, i.e., the spread of sea temperature occupied by a species; Burrows et al. 2019).

To calculate the STI of each canopy-forming species, we downloaded all Fucales and Laminariales presence records from the ATLAS of Living Australia—which contains data on herbarium specimens and government monitoring programmes, as well as the Australian Temperate Reef Collaboration and Shears and Babcock (2007), which represent the most comprehensive reef monitoring programmes in Australia and New Zealand, respectively. To fill spatial data gaps across Western Australia, where the marine flora is relatively understudied due to the vastness and remoteness of the coastline, we extracted additional species distribution records from Bennett et al. (2015); Colman (1997); and Pessarrodona and Grimaldi (2022). Records well outside the recorded distribution described in Womersley (1987) and Huisman (2015) were removed, as these studies represent the most comprehensive description of the temperate and tropical Australian flora to date. For each presence-record, daily sea surface temperature (SST) records from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation SST data set (version 2.1, OISST v2.1, Huang et al. 2021) were extracted from the nearest grid cell (nearest neighbour, 0.25° × 0.25°) from September 1981 to January 2023. The mean SST value of each distributional record was then calculated across the 42-year time series for each location. Sampling effort in the species distribution data set was concentrated towards accessible locations and cities (Figure S2), which are not representative of the vast remote Australian coastline. To minimise spatial autocorrelation, the SST of distribution records was pooled within 0.5° × 0.5° latitude × longitude grid cells and their temperature was averaged. The thermal distribution was then calculated by taking the minimum and maximum average SST of the grid cells, and the thermal midpoint taken as the midpoint of this range (Table S1).

Finally, we also compared the relationship between the mean changes in relative abundance of each species, their STI and their relative position in their range—the thermal range index (TRI, Bennett et al. 2022). The range index was calculated as:

TABLE 1 | Details of the survey sites in the studied locations.

Site	Substratum	Depth (m)	Historical survey	Resurvey	Response variable	References
Hamelin Bay						
Peak Island	Limestone	5–10	February 1999	February 2024	Dry biomass	Kendrick et al. (1999)
Hamelin Island	Limestone	5–8				
Foul Bay (inshore)	Granite	8				
Foul Bay (offshore)	Limestone	6–10				
Cosy Corner	Limestone	8	December 2005		Fresh biomass	Westera et al. (2007)
Cosy Corner 2	Limestone	10	February 2006		Fresh biomass	Babcock et al. (2006)
Bremer Bay						
Peppermint Beach South	Granite	7	March 1997	April 2023	Percent cover	Colman (1997)
Black point E	Granite	8				
Black Point W	Granite	8				
Glasse Island	Granite	8				
James Cove	Limestone	10				
Bremer Bay Point	Granite	6				
Esperance Bay						
Black Island	Granite	< 10, 10–20	October 2002	April 2021 (Exposed), April 2023 (Sheltered)	Fresh biomass	Goldberg and Kendrick (2004)
Woody Island	Granite					
Thomas Island	Granite					
Remark Island	Granite					
Frederick Island	Granite					
Long Island	Granite					

$$2 \cdot \frac{\mathrm{SM} - \mathrm{STI}}{\mathrm{STR}}$$

where SM is the median temperature at the grid cell where the experimental collection site was located, STI is the species thermal index and STR is the species thermal range. The RI scales from −1 to 1, whereby −1 represents the cool edge of a species distribution, '0' represents the thermal midpoint and 1 represents the warm edge. The relative change in abundance was estimated as:

$$\frac{\overline{X}\mathrm{c} - \overline{X}\mathrm{h}}{\overline{X}\mathrm{c} + \overline{X}\mathrm{h}} \cdot 100$$

where $\overline{X}$ is the mean abundance (biomass or percent cover) across quadrats at each site in contemporary ($\overline{X}$c) and historical ($\overline{X}$h) surveys. Relative abundance change thus ranged from −100 (total loss) to 100 (appearance).

2.5 | Statistical Analyses

In each location, temporal differences in the total canopy abundance, the abundance of morphofunctional groups and the CTI, CTDiv and CTR of shallow (< 10 m) reefs were examined with generalised linear mixed models (GLMMs) within the R statistical environment using the GLMMTMB package (Brooks et al. 2017). Locations were examined separately as historically they did not have the same response variable (i.e., biomass or cover of canopy-forming algae). GLMMs were fitted with a Gaussian (CTI, CTDiv, CTR, total canopy biomass in Hamelin) or a tweedie (rest of models) distribution when exploration of the residuals revealed heteroscedasticity of the residuals and non-normality. During the resampling of the exposed reefs of Esperance Bay in 2021, *Sargassum, Phyllotricha and Sargassopsis* spp. could not be identified to species level, so a genus-wide STI of the species occurring in Australasia was used to calculate the community thermal metrics (CTI, CTDiv and CTR). Species-specific STIs were used in the other locations/models. Model fit was assessed with the DHARMA package (Hartig 2020). In all our models, 'sampling year' was treated as a fixed effect (2 levels) and 'site' as a random effect (6 levels) in order to account for variability introduced by differences between the sites that could otherwise confound patterns of change across time. To assess temporal shifts in the species composition of forest canopies in each location, we used a permutational analysis of variance (PERMANOVA) based on Bray–Curtis distances of square-root transformed biomass data (wet weight). Our analysis conducted 9999 unrestricted permutations of the raw data using PRIMER 7.0 with the PERMANOVA + add-on (Anderson, Gorley, and Clarke 2008). Site was included as a random factor nested within location, to account for the hierarchical nature of the data. We conducted permutational analysis of multivariate dispersion (PERMDISP) to determine whether within-group variation differed between levels of each factor. Finally, similarity percentage analysis (SIMPER) was used to identify which species/taxa were responsible for the similarity between years. In Esperance Bay, we also included the factors exposure (fixed, 2 levels) and depth (fixed, 2 levels). In the model examining temporal change across exposure and depths in Esperance Bay, species of *Sargassum, Phyllotricha and Sargassopsis* were grouped under one taxonomic category as they could not be identified to species level during the 2021 resampling of the exposed reefs.

3 | Results

3.1 | Change in Shallow Sheltered Reefs

Overall, the sheltered shallow seaweed forests we sampled across the south coast of Australia showed little change in total canopy cover or total biomass over time (GLMM, p-value > 0.05, Figure S3). There were no significant differences in overall canopy species composition over time in Hamelin and Bremer Bay (PERMANOVA, p-value > 0.05, Table S2), but some group-specific changes were detected over time in some locations (Tables 2 and S2). A significant increase in the dominant kelp species *Ecklonia radiata* was detected in Hamelin Bay when trends were examined individually for each morphofunctional group (Figure 2A, GLMM, estimate = 0.029, SE = 0.01, $p < 0.05$). A decrease in the overall abundance of *Cystophora* spp. was detected in Bremer Bay (percent cover; GLMM, estimate = −0.680, SE = 0.16, $p < 0.001$) and Esperance Bay (Figure 2B,C; GLMM, estimate = 0.532, SE = 0.171, $p < 0.01$). Canopy species composition was marginally significantly different in Esperance Bay (PERMANOVA, $p = 0.043$, Table S2). Here, dissimilarity between years was driven primarily by a significant decrease in several *Cystophora* species (e.g., *C. expansa*, *C. brownii*, *C. gracilis*, *C. subfarcinata*, Figure 2B,C; Table 2) and moderate increases in *Sargassum* spp. (e.g., *Sargassum spinuligerum*, *Phyllotricha decipiens*, Figure 2, Table 2, GLMM, estimate = −0.824, SE = 0.367, $p < 0.05$) and other canopy-forming fucoids (*Acrocarpia robusta*, GLMM, estimate = −0.626, SE = 0.301, $p < 0.05$). There was an increase in *Cystophora polycystidea*, which was largely absent from the 2002 surveys.

3.2 | Change Across Depths and Wave Exposures

Our hierarchical sampling design in Esperance Bay revealed that species composition varied strongly across depth and exposure (PERMANOVA, $p < 0.05$, Table S3, Figure 3). Shallow depths had greater biomass of *Cystophora* spp., *Sargassum* spp. and *Acrocarpia robusta*, while species like *Ecklonia radiata* or *Scytothalia dorycarpa* were more abundant between 10 and 20 m (Figure 3). These two species were also more abundant on wave-exposed reefs, which featured fewer *Cystophora* spp. On average across all sites, the strong community structuring across depth and exposure persisted over time (non-significant Year × Exposure, and Year × Depth interactions, $p > 0.25$ and $p > 0.5$, respectively). Some specific sites did show significant changes between years however (significant Year × Site interaction, $p < 0.001$), including site-specific temporal changes in canopy structure across depths and exposures (significant Year × Site × Depth, Year × Site × Exposure and Year × Site × Depth × Exposure interactions, $p < 0.001$). These changes were mostly driven by increases in *Ecklonia radiata* and *Scytothalia dorycarpa*, and the decline of several (but not all) *Cystophora* spp. (e.g., *Cystophora subfarcinata, Cystophora gracilis, Cystophora racemosa*) at some sites like Frederick or Woody Island (SIMPER, Table 2).

TABLE 2 | Breakdown of average dissimilarity between historical and contemporary sampling events at the studied locations contributed by each canopy taxa and their thermal index (STI); taxa are ordered in decreasing contributions.

Species	STI (°C)	Average historical abundance	Average contemporary abundance		Av. Diss	Diss/SD	Contrib%	Cum.%
Hamelin Bay < 10 m								
Ecklonia radiata	16.93	14.31	24.79	▲	28.52	1.17	36.93	36.93
Scytothalia dorycarpa	18.04	6.08	11.23	▲	26.04	0.79	20.78	57.71
Platythalia quercifolia	19.86	9.88	1.12	▼	12.44	0.67	16.11	73.83
Cystophora racemosa	17.72	3.30	2.39	▼	5.82	0.54	7.54	81.37
Cystophora moniliformis	16.28	2.31	1.32	▼	2.99	0.36	3.88	85.24
Cystophora harveyi	19.33	1.67	0.71	▼	2.64	0.41	3.41	88.66
Bremer Bay < 10 m								
Sargassum spp.	16.73	1.49	1.42	▼	13.06	0.83	19.9	19.9
Scytothalia dorycarpa	18.04	0.73	0.94	▲	11.84	0.91	18.03	37.93
Ecklonia radiata	16.93	0.7	0.87	▲	11.13	0.92	16.96	54.88
Cystophora monilifera	16.80	0.53	0.21	▼	6.73	0.67	10.25	65.14
Cystophora pectinata	17.25	0.52	0.37	▼	6.71	0.76	10.22	75.35
Cystophora racemosa	17.72	0.17	0.3	▲	4.04	0.53	6.15	81.5
Cystophora expansa	16.91	0.2	0.09	▼	2.67	0.41	4.07	85.57
Esperance Bay < 10 m								
Cystophora expansa	16.91	2.35	0.98	▼	7.03	1.06	9.95	9.95
Cystophora brownii	17.26	2.46	2.39	▼	6.89	1.21	9.76	19.71
Acrocarpia robusta	18.83	0.89	2.18		6.1	1.17	8.63	28.34
Phyllotricha verruculosa	15.40	1.16	1.15	▼	4.37	1.2	6.19	34.53
Cystophora gracilis	17.95	1.23	0.69	▼	4.06	0.97	5.75	40.27
Sargassum spinuligerum	17.6	1.36	1.62	▲	3.89	1.22	5.5	45.77
Phyllotricha varians	15.42	1.03	1.16	▲	3.75	1.15	5.31	51.08
Phyllotricha decipiens	15.58	0.6	1.25	▲	3.73	0.98	5.28	56.36
Cystophora polycystidea	15.63	0	1.28	▲	3.65	0.83	5.16	61.52
Sargassum linearifolium	18.31	0.41	0.8	▲	3.48	0.66	4.93	66.45
Scaberia agardhii	16.90	0.96	0.14	▼	3.38	0.57	4.79	71.24
Sargassum sargassum	18.49	1.06	0	▼	3.27	0.91	4.63	75.87
Cystophora subfarcinata	15.63	1.09	0.13	▼	3.23	0.7	4.57	80.44
Sargassum spp.	16.73	1.1	0.14	▼	3.17	1.11	4.49	84.93
Esperance Bay (all sites)								
Ecklonia radiata	16.93	0.51	1.47	▲	8.15	0.71	11.73	11.73
Sargassum spp.	16.73	2.69	2.85	▲	8.07	1.09	11.61	23.34
Scytothalia dorycarpa	18.04	0.57	1.25	▲	7.83	0.63	11.26	34.6
Cystophora brownii	17.26	0.8	0.99	▲	6.71	0.79	9.66	44.25
Cystophora monilifera	16.80	0.82	0.82		6.43	0.74	9.25	53.51

(Continues)

TABLE 2 | (Continued)

Species	STI (°C)	Average historical abundance	Average contemporary abundance		Av. Diss	Diss/SD	Contrib%	Cum.%
Acrocarpia robusta	18.83	0.56	1.12	▲	6.38	0.75	9.18	62.69
Cystophora expansa	16.91	0.72	0.81	▲	5.69	0.7	8.19	70.87
Cystophora racemosa	17.72	0.54	0.5	▼	4.14	0.51	5.96	76.83
Cystophora pectinata	17.25	0.25	0.48	▲	2.9	0.46	4.17	81
Cystophora gracilis	17.95	0.47	0.29	▼	2.79	0.54	4.01	85.02

Notes: Only taxa contributing at least 3% are included. Note the abundances (biomass or percent cover) were square root transformed for analysis. Green arrows indicate increases in mean abundance over time while red arrows denote decreases.

3.3 | Change in Community Thermal Affinity

The CTI of forest canopies remained stable throughout the sampling period in Bremer Bay and Esperance (LMM, $p = 0.22$ and $p = 0.46$, respectively; Figure 4) and significantly decreased between the sampling periods in Hamelin Bay (LMM, $p = 0.03$, Figure 4A). This decrease was largely driven by the decline of warm-affinity *Platythalia quercifolia* and *Cystophora harveyi*, both Western Australian endemics with a relatively high STI, and the increase of *Ecklonia radiata*, which has a relatively lower STI (Tables 2 and S1). In Esperance Bay, the CTI did not differ significantly with time or depth (LMM, $p = 0.5$ and $p = 0.3$, respectively), but the CTI of exposed reefs was significantly higher (~18.2°C, LMM, $p < 0.001$) than shallow sites (~17.8°C, Figure 4C). The variability in thermal affinities among species (CTDiv) also did not significantly change over time at any of the studied locations (LMM, $p > 0.05$; Figure 4D,E). Across local scale gradients of exposure in Esperance Bay, sheltered sites had significantly lower CTDiv than exposed reefs (LMM, $p < 0.001$), but CTDiv did not vary with depth. The community thermal range (CTR) did not change over time at any of the locations (LMM, $p = 0.051$, $p = 0.056$, $p = 0.91$, respectively). Sheltered sites had significantly lower CTR than exposed sites in Esperance Bay (LMM, $p < 0.001$ and $p = 0.038$, respectively) and shallow sites had significantly lower CTR than deeper sites (LMM, $p < 0.001$).

Overall, any observed relative changes in the relative abundance of a canopy species had little relationship to their thermal midpoint (STI), or their position within their realised thermal range (TRI; Figures S4 and S5). In Hamelin and Bremer Bay, there was no relationship between a species' STI or their thermal range index and change in their average site relative abundance over time (Figures S4A,B and S5A,B). Sites in Esperance Bay also did not show a relationship between species-level abundance change and STI or range index, with the only exception of a negative correlation at the exposed sites at 15 m depth (Figures S4C and S5C), suggesting that, counter to the observed warming trend, warm-affinity species had decreased in abundance.

4 | Discussion

The marine forest canopies along the western south coast of Australia appear to have changed relatively little over the last two decades, a period where the intensity of coastal warming (~0.14°C decade^{-1}; Figure 1) has been on par with other regions globally (Bureau of Meteorology 2022). Remarkably, forest' total biomass and species composition remained largely unchanged even in locations that have experienced a +2°C monthly climatological maximum anomaly during the study period (e.g., Hamelin Bay), which does not support our first hypothesis (changes will reflect the intensity of gradual and extreme warming). This was surprising considering this area constitutes the warm range edge of several species (Figures S1 and S5). Seaweed forests throughout the region were strongly structured over wave and depth gradients, but there was also little change in canopy total biomass or species composition over these gradients between the sampling periods, also refuting our second hypothesis (community changes will be greater in shallow sheltered reefs than in exposed deeper reefs). The only significant change across some locations was the increase in density, cover and biomass of the kelp *Ecklonia radiata*, the dominant species on other coastlines, and a decrease in several *Cystophora* species in shallow reefs. This is consistent with patterns observed along the ocean temperature gradient of the west coast (Wernberg et al. 2011)—where *Cystophora* spp. in the warmer locations have become functionally extinct during the last 50 years (Pessarrodona 2022), as well as with future predictions based on species distribution models (Martínez et al. 2018). Our third hypothesis was also not supported, as changes were largely irrespective of species thermal affinity or position in their thermal range. Overall, our findings suggest that forests of southwest Australia have persisted in a relatively unaltered state for the last 20–25 years, which offers a valuable opportunity to establish a baseline of the role these remote and understudied habitats play in supporting biodiversity and ecosystem functioning. The non-linear trajectories that many temperate reef communities have shown in response to warming, whereby relative stability is followed by abrupt change (McPherson et al. 2021; Soler et al. 2022; Starko et al. 2022; Wernberg et al. 2016), calls however for a better understanding of their response to anthropogenic threats.

4.1 | Change in Shallow Sheltered Reefs

The apparent seaweed forest stability we observed across all study locations contrasted with the spatial footprint of warming and extreme events experienced in southern Australia since the time of historical sampling, and may be explained by two non-mutually exclusive hypotheses: (i) the intensity of stress and disturbance

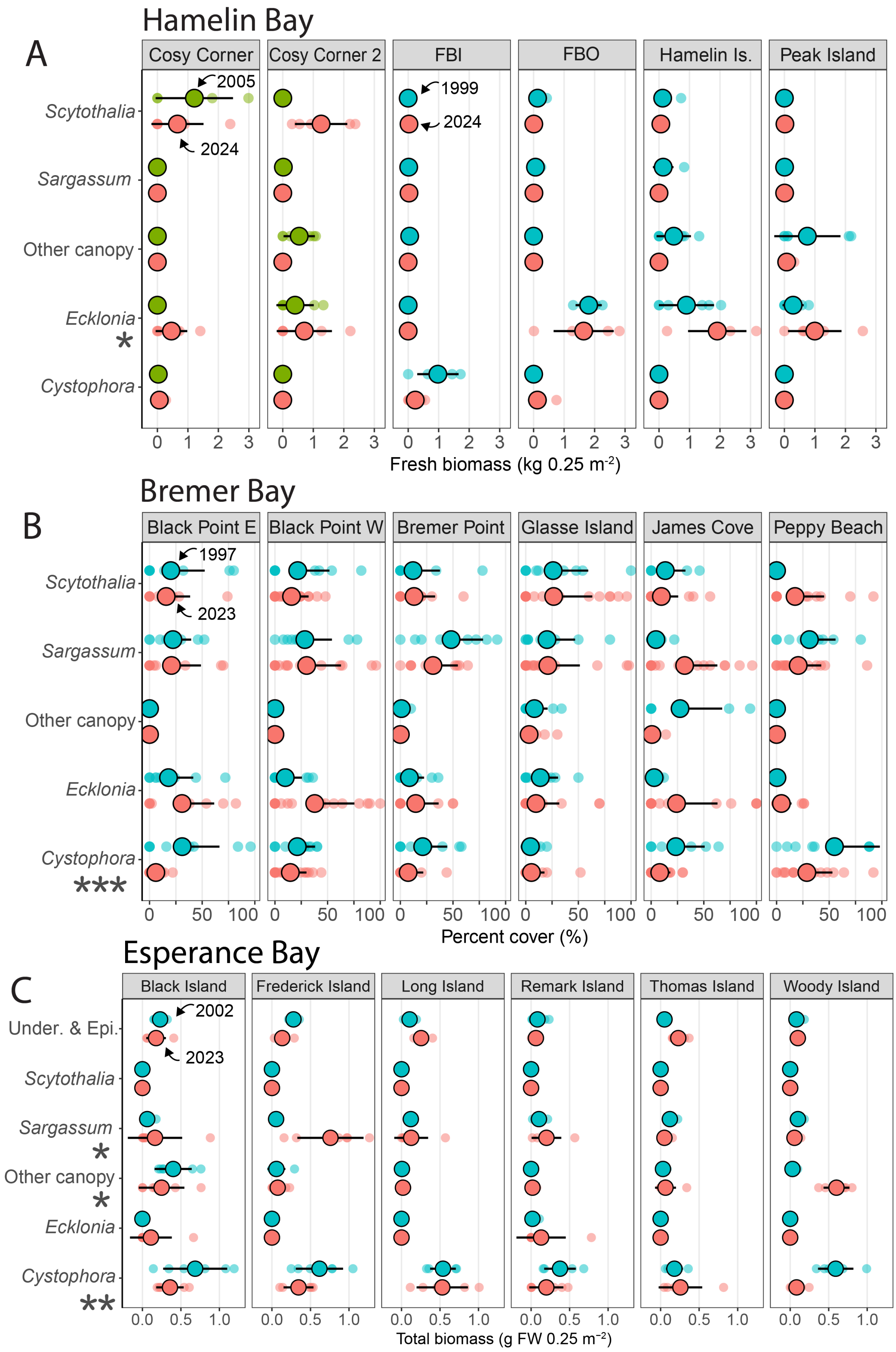

FIGURE 2 | Biomass change of different canopy groups (genera) over the two sampling periods at shallow (<10 m) sheltered subtidal reefs. Small dots show the quadrat-level biomass (Hamelin and Esperance Bay, $n = 6$) or cover (Bremer Bay, $n = 10$–20) within each site, while larger dots and error bars denote the mean and standard deviation (SD). Asterisks denote significant differences in the biomass or cover of individual morphofunctional groups between years (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Under. and Epi., understorey and epiphytes.

FIGURE 3 | Total biomass of different canopy groups (genera), understorey and epiphytes (Und. and Epi.) at different depths (5 and 15 m) and years at sheltered (A, leeward side) and exposed (B, windward side) of multiple islands in Esperance Bay. Small dots show the quadrat-level biomass ($n = 6$) within each site, while larger dots and error bars denote the mean and standard deviation (SD). Under. and Epi., understorey and epiphytes.

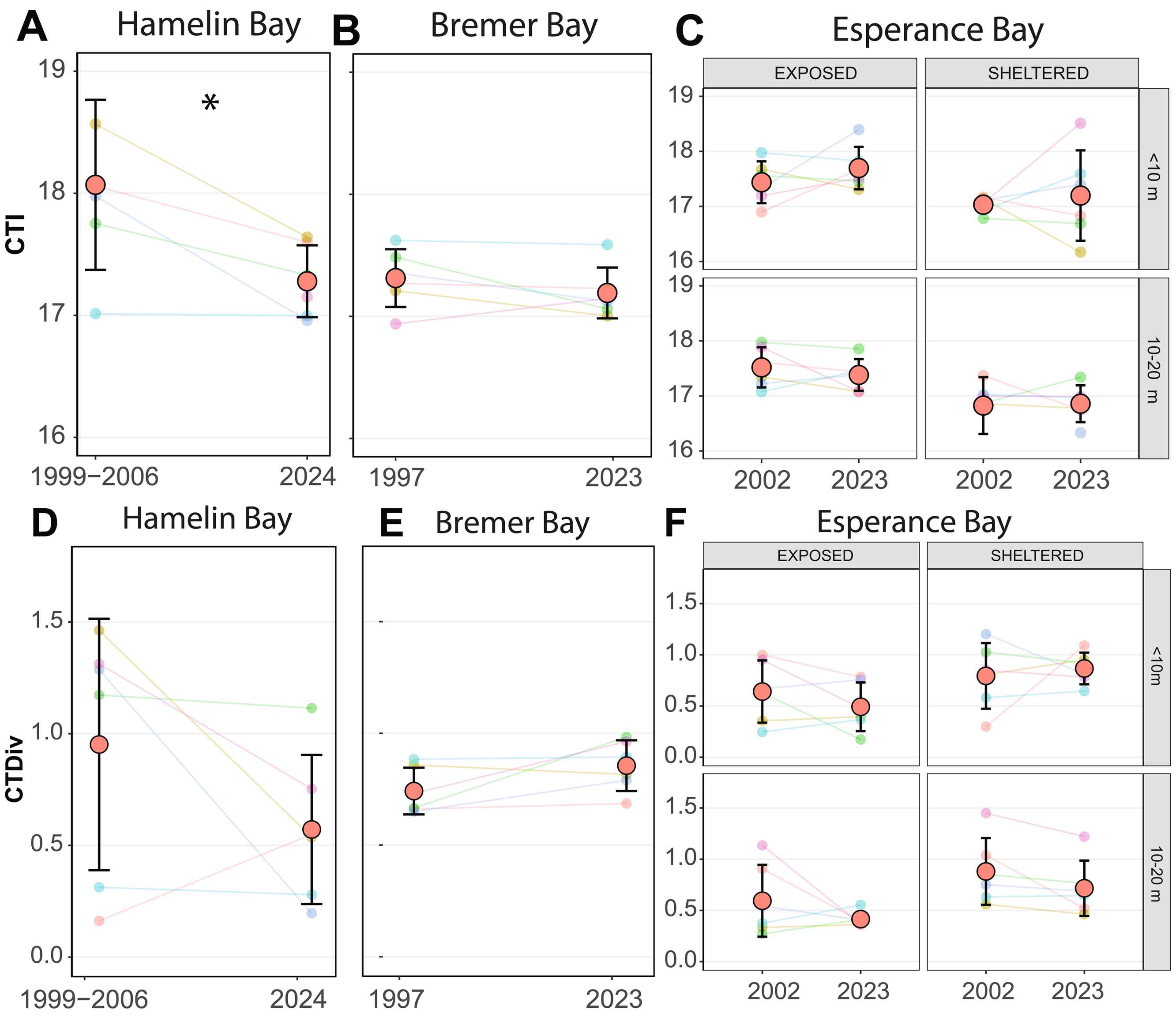

FIGURE 4 | Trends in community thermal index (CTI) and community thermal diversity (CTDiv) at Hamelin, Bremer and Esperance Bay over time. Temporal trends in Esperance Bay are shown across different exposures and depths. Coloured dots and lines indicate different sites. Asterisks denote significant differences in CTI or CTDiv over time (*$p < 0.05$).

events (e.g., warming, nutrient pollution, storms) has not been large enough to drive forest change; and/or (ii) a relatively high resilience of these forests to change and disturbance. Increased nutrient and sediment inputs have driven seaweed forest losses in southern Australia (Connell et al. 2008; Gorman, Russell, and Connell 2009; Shepherd et al. 2009), but these appear minimal in the western south coast. Urbanisation in the study area has remained minimal over the last two decades (2021 Census, Australian Bureau of Statistics), and the lack of river discharge and little agricultural land cover change over the past decade suggest that nutrient run-off has remained stable over time (Department of Water and Environmental Regulation 2011, 2019). The increase in average sea surface temperatures (+0.3°C, 2000–2023) recorded in the western south coast of Australia is lower than other temperate regions where warming has caused forest losses and species reconfiguration (e.g., Japan, +0.95°C, 1970–2009, Tanaka et al. 2012; Spain, +0.69°C, 1982–2014, Arriaga et al. 2024). For instance, Tasmanian forest communities were relatively stable during a period of slight warming (+0.12°C; 1990 to mid-2000s), but experienced a general decline in cover and an increase in warm-affinity species during more pronounced warming (+0.68°C; 2010s to present; Soler et al. 2022). These observations suggest that the rate amount of warming observed within this shorter study period may not have exceeded the thermal safety margins of the species/populations examined. This is especially likely in Bremer and Esperance Bay, where maximum sea surface temperatures have remained more stable (Figure S6). It is worth noting, however, that the underlying drivers of ecosystem structure are often determined by short-term weather events (e.g., marine heatwaves), as these disproportionately affect species mortality, growth and reproduction (Helmuth et al. 2014). In that sense, the little community change observed in our warmest location, which experienced a +2°C monthly climatological maximum anomaly, is still surprising.

The apparent stability of the studied forest communities over time may also be explained by a relatively high resilience to disturbance. Species and trait-diverse communities are expected to have higher resilience to environmental fluctuations (MacArthur 1955; Naeem and Li 1997), so that ecosystem properties like total canopy biomass are stable because declines in the biomass of some species are offset by increase in others (Yachi and Loreau 1999). Forest canopies of the western south coast of Australia have extreme high alpha, beta, and gamma diversity by global standards, commonly consisting of > 10 species in a single stand (Collings 1996; Goldberg and Kendrick 2004; Pessarrodona and Grimaldi 2022). This diversity is the result of several interacting processes. High microhabitat complexity in the studied reefs allows for species to occupy slightly different niches (Toohey, Kendrick, and Harvey 2007), reducing competition and long-term exclusion; recurrent physical disturbances to the canopy (Kendrick et al. 2004) and year-round availability of propagules for colonisation (Emmerson and Collings 1998; Hotchkiss 1999; Pessarrodona and Grimaldi 2022) reduces a species' ability to competitively exclude others (Goldberg and Kendrick 2005; Hotchkiss 1999; Shepherd and Womersley 1981; Turner and Cheshire 2003) allowing for high diversity. A high degree of functional redundancy and ecosystem resilience to disturbance can thus be expected of these canopies (Biggs et al. 2020). At the species level, it is possible that high genetic diversity and physiological versatility buffers the response of seaweed species to climate change impacts (Wernberg et al. 2018; Vranken et al. 2021).

4.2 | Change Across Depths and Exposures

Forest composition significantly varied across depth and exposure, which agrees with previous studies from southern Australian forests (Collings and Cheshire 1998; Goldberg and Kendrick 2004; Shepherd and Womersley 1981; Wernberg and Connell 2008). South-western Australia has some of the highest wave energy in the world (Cuttler, Hansen, and Lowe 2020), with only a few wave-adapted species (*Ecklonia radiata*, *Scytothalia dorycarpa*) being able to tolerate the most wave-exposed habitats (Figure S7). The relative increase in *Ecklonia radiata* across some sites could be related to the strengthening of the wave conditions that has occurred in the region since the early 2000s (Cuttler, Hansen, and Lowe 2020). Indeed, *Ecklonia radiata* in particular is a strong competitor which is able to colonise storm-created canopy gaps and exclude most species after 3 years (Toohey, Kendrick, and Harvey 2007).

4.3 | Change in Community Thermal Affinity

Another key finding of our study is that most changes in species-level abundance occurred irrespective of their thermal affinity. This was the case even in locations like Hamelin Bay, where maximum sea surface temperatures neared the upper realised thermal distribution limits of species (e.g., 24°C for *Cystophora* spp., Figures S1 and S8; Martínez et al. 2018). It is possible that the species temperature index or the thermal range index where not sensitive enough to pick up small thermal affinity differences between species, or that the indices fail to capture the thermal tolerance and affinity of the species studies here. This could be due to species having a higher thermal performance than their realised thermal distribution (e.g., as a result of deep evolutionary legacies, Bennett et al. 2022), or strong local adaptation affecting species responses to warming. Preliminary seascape genomics data suggest that *Cystophora* populations show strong local genetic structuring (Wood et al., unpublished data), which could result in range edge populations having higher thermal tolerance than populations found in the centre or edge of their range (Wood et al. 2021). Similarly, strong local adaptation has been documented in *Scytothalia dorycarpa* and *Ecklonia radiata* (Bennett et al. 2015; Vranken et al. 2021). Better constraining the adaptive genetic capacity and the phylogeography of the rich canopy assemblages studied here will help further unpack the observed patterns.

At the community level, the average thermal affinity of the canopy (i.e., the CTI) did not track ocean warming, and warm- and cool-affinity species both increased and decreased in forest canopies. The CTI of marine communities often tracks warming (Arriaga et al. 2024; Soler et al. 2022), but species nonlinear responses to changes in temperature can result in nonlinear relationships between CTI and temperature (Flanagan et al. 2019). The low CTI sensitivity of southern Australian forest canopies to warming may be explained by their low community thermal diversity (CTDiv), as communities with low CTDiv have species with similar thermal affinities and higher 'thermal affinity redundancy' (Burrows et al. 2019). Indeed, the historical CTDiv of the examined communities (0.67 ± 0.14°C, 0.62 ± 0.05°C, 0.79 ± 0.1°C for Hamelin, Bremer and Esperance Bay, respectively; mean ± SE) lies in the low range of values reported in the literature (e.g., 0.93°C and 2.48°C for intertidal seaweed forests in Shetland and southwest Britain, respectively; Burrows et al. 2020). Importantly however, southern Australian forests had a relatively narrow community thermal range (CTR), suggesting that community wide declines in species performance and abundance may occur rapidly once thermal ranges are exceeded. Our results also suggest that this change may be greater in exposed reefs, where there was higher variability in thermal affinities among species (i.e., significantly higher CTDiv).

A useful way to examine the vulnerability of a species or community to temperature is to look at their thermal bias, that is, the difference between the CTI and the local temperature. The community thermal affinity of forests in the cooler location (Esperance Bay) largely matched contemporary sea surface temperatures (i.e., no thermal bias), and experienced no consistent directional change with time, further evidencing that other abiotic (e.g., wave exposure, depth) and biotic (e.g., species turnover) are likely more important drivers of contemporary community structure. In contrast, the community thermal affinity of forests in the warmest location (Hamelin Bay) was cooler than present temperatures, suggesting a greater vulnerability to warming. Such negative thermal bias may be explained by the important component of South Australian marine flora which has cool-temperate origins (Kendrick et al. 2009; Phillips 2001), with the marine forest canopies of Australia and Antarctica presumably having had similarly rich fucoid diversity before the Eocene (Clayton 1994). Importantly, thermal bias in the warmest location consistently increased by 0.05°C–1.02°C across sites over time (Figure 5), pointing to an increase in thermal vulnerability. It is possible that future thermal anomalies may reshuffle species composition to align with current temperatures, as previously occurred in the west coast, where temperate communities with the greatest negative thermal bias where

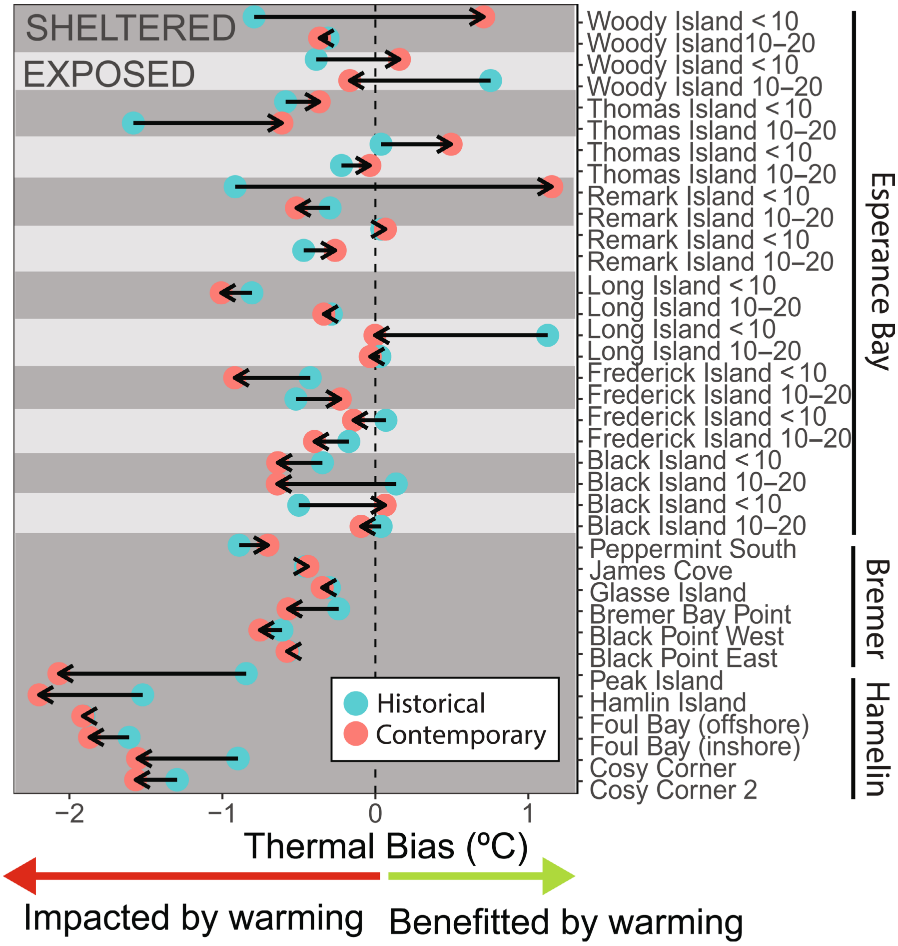

FIGURE 5 | Community thermal bias of canopy forests across sampled sites in the southwest coast. Sites are grouped according to location and wave exposure. Numbers indicate depth (< 10 m, 10–20 m). Communities with a positive thermal bias are expected to have reduced sensitivity to warming, while communities with a negative thermal are expected to be vulnerable to warming-driven species reshuffling.

replaced by subtropical and tropical species once species thermal thresholds were exceeded (Wernberg et al. 2016).

Our analyses should be considered relatively robust as they had a large degree of spatial replication. The remote nature of the study sites, however, confined the sampling to two temporal points. Although such two time-point analyses lack the temporal resolution to detect inter-annual fluctuations in standing biomass and community composition, these are relatively minor in Australian subtidal fucoid forests (Babcock et al. 2006; Collings 1996; Hotchkiss 1999; Kirkman 1984; Wernberg and Goldberg 2008; Westera et al. 2007). As such, two time-point analysis can still be useful to identify broad changes in data-poor species like the ones studied here (Csordas et al. 2024). Indeed, although sampling time points differed by multiple years across locations, patterns were largely consistent. Most of our surveys were conducted at similar seasons than the historical surveys (Table 1), limiting the strong seasonal variation in canopy biomass that is known to drive changes in understorey species biomass and overall community composition (Wernberg and Goldberg 2008; Babcock et al. 2006; Collings 1996; Goldberg 2005). The only exception was Esperance Bay (Table 1), where our autumn sampling detected higher abundances of kelps than in the historical sampling in spring. Kelp biomass peaks in late summer (Kirkman 1984), while peak biomass of fucoids like *Cystophora* occurs in spring (Goldberg 2005; Hotchkiss 1999; Pessarrodona and Grimaldi 2022). While the differential sampling times may have introduced bias in this instance, we detected a concurrent increase in adult kelp density (Figure S9), which typically exhibits minimal seasonal variation as it is a perennial species, suggesting that the observed increases in abundance are not solely an artefact of seasonal differences in biomass but also changes in the actual abundance of adult kelps.

The apparent lack of change in southern Australia over a period of ~20 years contrasts with observations globally and elsewhere in the Australian continent, where significant declines in forest cover and/or species composition have been recorded in recent decades (Butler et al. 2020; Coleman et al. 2008; Connell et al. 2008; Shepherd et al. 2009; Smale 2019; Soler et al. 2022). In particular, our findings contrast with those from the neighbouring west and eastern/central south coasts, where temperate reef communities have undergone substantial change since the last mid-century, mostly due to climate change and urbanisation (Bennett 2015; Connell et al. 2008; Pessarrodona 2022; Wernberg et al. 2013). Albeit more poorly studied, Australian tropical seaweed communities also appear to be rapidly changing (Phillips and Blackshaw 2011). This underscores the need for a more comprehensive geographic sampling to inform our view of regional and global change, as trends in remote locations may not necessarily agree with those from more well-studied areas. Our findings also highlight the conservation value of remote seaweed forests, which may constitute relatively pristine reservoirs of biodiversity within broader regionally changing contexts. The western south coast of Australia emerges as a particularly valuable example, given that its forests harbour numerous endemic species and a substantial fraction of the world's deep phylogenetic diversity (Coleman and Wernberg 2017; Pessarrodona and Grimaldi 2022). With warming and other anthropogenic threats to coastal marine ecosystems predicted to increase globally however, continuous monitoring of Australian marine forests is needed to create an understanding of change. Furthermore, the thermal safety limits of most Australian forest-forming species and populations remain unknown, and future experimental thermal performance studies are needed to predict future vulnerability as well as better explain any potential stability.

Author Contributions

Albert Pessarrodona: conceptualization, formal analysis, data curation, investigation (2020s), visualization, writing – original draft, writing – review and editing, funding aquisition (2020s). **Georgina Wood:** investigation (2020s), funding aquisition (2020s), writing – review and editing. **Camille M. Grimaldi:** investigation (2020s), formal analysis, writing – review and editing. **Nisse Goldberg:** investigation (2000s), funding aquisition (2000s), writing – review and editing. **Gary A. Kendrick:** investigation (2000s), funding aquisition (2000s), writing – review and editing. **Samuel Starko:** funding aquisition (2020s), writing – review and editing. **Thomas Wernberg:** investigation (2020s), supervision, funding aquisition (2020s), writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code are archived in the Figshare repository (Pessarrodona et al. 2024).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13933.

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Supporting Information

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