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Microbial tropicalization driven by a strengthening western ocean boundary current

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Abstract

Western boundary currents (WBCs) redistribute heat and oligotrophic seawater from the tropics to temperate latitudes, with several displaying substantial climate change-driven intensification over the last century. Strengthening WBCs have been implicated in the poleward range expansion of marine macroflora and fauna, however, the impacts on the structure and function of temperate microbial communities are largely unknown. Here we show that the major subtropical WBC of the South Pacific Ocean, the East Australian Current (EAC), transports microbial assemblages that maintain tropical and oligotrophic (*k*-strategist) signatures, to seasonally displace more copiotrophic (*r*-strategist) temperate microbial populations within temperate latitudes of the Tasman Sea. We identified specific characteristics of EAC microbial assemblages compared with non-EAC assemblages, including strain transitions within the SAR11 clade, enrichment of *Prochlorococcus*, predicted smaller genome sizes and shifts in the importance of several functional genes, including those associated with cyanobacterial photosynthesis, secondary metabolism and fatty acid and lipid transport. At a temperate time-series site in the Tasman Sea, we observed significant reductions in standing stocks of total carbon and chlorophyll *a*, and a shift towards smaller phytoplankton and carnivorous copepods, associated with the seasonal impact of the EAC microbial assemblage. In light of the substantial shifts in microbial assemblage structure and function associated with the EAC, we conclude that climate-driven expansions of WBCs will expand the range of tropical oligotrophic microbes, and potentially profoundly impact the trophic status of temperate waters.

KEYWORDS
East Australian Current, microbial community, microbial indicators, ocean boundary currents, tropicalization

1 | INTRODUCTION

As the primary agents of planktonic dispersal, ocean currents are intricately linked to the biogeographical ranges of marine species (Baltazar-Soares et al., 2014; Barton, Dutkiewicz, Flierl, Bragg, & Follows, 2010; Kingsbury, Gillanders, Booth, & Nagelkerken, 2020; Lévy, Jahn, Dutkiewicz, & Follows, 2014; Scott, Marsh, & Hays, 2014). Consequently, climate change-driven shifts in ocean current dynamics have important impacts on species movements, which in turn affect regional metacommunity composition (or species pools; Pecl et al., 2017). The impacts of changing current dynamics may be more profound where they span transitional zones in species distributions (Poloczanska et al., 2013; Sorte, Williams, & Carlton, 2010). Indeed, poleward range shifts are a well-documented consequence of the impact of climate change on marine species, with the expansion of the distribution of marine taxa in response to climate change estimated to be on average 72 km per decade, and as high as ~142 and 470 km for pelagic zooplankton and phytoplankton respectively (Poloczanska et al., 2013).

Climate change-driven shifts in ocean current dynamics have repeatedly been observed at the western edges of the ocean basins (Cai, 2006; Wu et al., 2012), where the western boundary currents (WBCs) transport warm, low salinity, oligotrophic waters into temperate latitudes. WBCs, including the Gulf Stream, the Kuroshio Current, the Agulhas Current, the Brazil Current and the East Australian Current (EAC), are narrow, rapid, wind-driven currents that profoundly shape the physical, chemical and biotic nature of the global ocean (Cai, 2006; Cai, Shi, Cowan, Bi, & Ribbe, 2005; Stommel, 1948; Wu et al., 2012). For instance, WBCs influence ocean to atmosphere heat and moisture fluxes, and ultimately impact meteorological phenomena and ocean carbon uptake (Hu et al., 2015; Kelly et al., 2010; Kwon et al., 2010; Minobe, Kuwano-Yoshida, Komori, Xie, & Small, 2008).

Emerging evidence suggests that the strength and influence of several WBCs are increasing as a consequence of shifting circulation patterns linked to climate change (Cai, 2006; Wu et al., 2012). For example, increased wind stress over the Pacific Ocean has enhanced the flow of the WBC of the South Pacific, the EAC, leading to a 350 km southerly expansion of its warm water flows into the temperate Tasman Sea since the 1940s (Cai et al., 2005; Ridgway, 2007; Wu et al., 2012). Prolonged (>250 days) and intense (+2.9°C) marine heatwaves in the region have also been attributed to the increasing southerly flow of the EAC (Oliver et al., 2017). In fact, due to the increasing strength and intensity of the EAC, sea surface temperatures in the Tasman Sea are warming at nearly four times the global ocean mean (Ridgway, 2007; Ridgway & Hill, 2009), making this region a global 'climate change hotspot' (Cai et al., 2005; Oliver et al., 2017; Oliver, Wotherspoon, Chamberlain, & Holbrook, 2014; Wu et al., 2012). Consequently, several macroscopic marine species, including benthic invertebrates (Ling, Johnson, Ridgway, Hobday, & Haddon, 2009), tropical and temperate fish (Figueira & Booth, 2010; Last et al., 2011), and some tropical phytoplankton species (Ajani, Allen, Ingleton, & Armand, 2014; Buchanan, Swadling, Eriksen, & Wild-Allen, 2014), have undergone poleward range shifts within south-eastern Australian marine waters, with substantial implications for the ecology of the impacted temperate regions (Vergés et al., 2014).

By virtue of their combined abundance (10^5–10^6 per millilitre of surface seawater), activity and metabolic diversity, marine microbes are responsible for the vast majority of biogeochemical transformations in the ocean ecosystem (Azam, 1998). They form the foundation of the marine food web and modulate the ocean's reservoirs and fluxes of carbon and climatically active gases, ultimately determining the *net* metabolic state of the ocean (Ducklow & Doney, 2012) and controlling global climate. However, marine waters are not homogenous. Gradients in physical, biogeochemical and climatic parameters provide strong selection on microbial assemblages resulting in both temporal and geographic partitioning of critical microbial processes across the global ocean (Ibarbalz et al., 2019; Salazar et al., 2019). That is, the direction and magnitude of biogeochemical transformations are constrained by the types of organisms present in the local community. Climate-related changes that alter physical mechanisms of microbial assembly in marine waters, including warming, stratification and shoaling of mixed layers, may therefore have broad-scale effects on biogeochemical cycles and food web dynamics, especially where they act to change the scale or mode (i.e. the type of organisms primarily responsible) of primary productivity (Flombaum, Wang, Primeau, & Martiny, 2020). The carbon fixed by cyanobacterial and pico-eukaryotic phototrophs can have different rates of sequestration or transfer to higher trophic levels than that fixed by larger phytoplankton such as diatoms, with potential concomitant impacts that cascade up to ecosystem level perturbation (Barton, Irwin, Finkel, & Stock, 2016; Bopp et al., 2001; Falkowski, Barber, & Smetacek, 1998; Henson, Le Moigne, & Giering, 2019).

The organismal traits that drive microbial distributions, such as capacity to utilize solar radiation (photosynthesis, proteorhodopsin, bacterial chlorophyll), fix nitrogen and adapt to ambient nutrient availability (trophic strategy) are strongly reflected in genomic content (Lauro et al., 2009) so that distinct ocean environments maintain a metabolic footprint that is imprinted on the genomic content of its microbial inhabitants (Gianoulis et al., 2009). As microbes generally lack defining phenotypic characteristics, and because individual organisms can be difficult to culture, molecular analyses, including taxonomically informative ribosomal DNA sequencing and

functionally informative metagenomic sequencing of mixed microbial assemblages from the environment provide a critical mechanism to study microbial dynamics.

While the impact of shifting WBC flow regimes on the macroecology of marine systems is beginning to become apparent, to date there is little understanding of how climate change-driven shifts in WBCs will influence the dynamics of the planktonic microbes that drive ocean productivity and global biogeochemical cycles. Investigations into bacterioplankton community structure and functional potential within WBCs are relatively limited (Focardi, Ostrowski, Goossen, Brown, & Paulsen, 2020; Phoma et al., 2018; Seymour et al., 2012), with the majority of research in this area focussed on characterizing nitrogen fixing prokaryotes in the Kuroshio Current (Cheung et al., 2017; Shiozaki et al., 2010, 2014, 2015, 2018). Although there is some evidence that physical advection of planktonic microbes can shape the process of community assembly (Barton et al., 2010; Cheung, Suzuki, Xia, & Liu, 2018; Galand et al., 2009; Shiozaki et al., 2015), the dynamics of microbial assemblages carried by surface currents through shifting environmental conditions are poorly defined outside of model simulations (Doblin & van Sebille, 2016). Theoretically, across multiple generations, microorganisms drifting within ocean currents may be transported >3,000 km into new environments (Doblin & van Sebille, 2016). Determining whether or not these cells transported from warmer locations can displace members of the microbial assemblage adapted to temperate conditions, and therefore elicit changes at the base of the marine food web, is key to understanding the implications of climate-driven changes on marine ecosystems.

Previous field studies of WBC microbial community dynamics and microbial advection have mostly focused on spatial point sampling (Doblin et al., 2016; Phoma et al., 2018; Seymour et al., 2012; Shiozaki et al., 2010, 2014, 2015, 2018), and have inferred dispersal through deep-water bodies that may remain isolated for tens to hundreds of years and where environmental conditions remain very stable (Agogué, Lamy, Neal, Sogin, & Herndl, 2012; Hamdan et al., 2013; Wilkins, van Sebille, Rintoul, Lauro, & Cavicchioli, 2013). Here we move beyond the general characterization of geographic distributions to employ a Lagrangian sampling approach coupled to time-series observations. Our aim was to deliver a detailed understanding of microbial community dynamics within the EAC and its surrounds by determining whether microbial community structure within the EAC is significantly distinct from the water surrounding it and by investigating to what extent microbial assemblages are transported in the WBC as it flows south. We also aimed to determine whether the impact of the EAC on temperate continental shelf ecosystems can be observed using microbial markers, and to suggest what specific impacts the anticipated strengthening of the EAC will have on these highly productive waters. In line with patterns observed in macroorganisms, we observed southerly incursions of warm EAC waters supporting the occurrence of tropically adapted microbial populations at higher latitudes, which correlated with significant transitions in productivity, biomass and community structure in higher trophic levels.

2 | MATERIALS AND METHODS

2.1 | Seawater sampling locations and protocols

2.1.1 | Oceanographic sampling

Sampling was conducted in October 2010 (Austral spring) during a voyage (ss2010_v09) aboard the *R/V Southern Surveyor* in waters off the continental shelf along the east coast of Australia. The EAC was identified using satellite-derived sea surface height and temperature, along with in situ water column temperature and acoustic Doppler current profiles. At the time of the study, the EAC was well defined, with both sea surface temperature and the current's southerly flow distinct from conditions in the surrounding water masses (Figure 1). Samples were collected over the course of 12 days and across two major study regions. The study regions incorporated (a) an ~50 hr Lagrangian drift, whereby the vessel was positioned within the body of the EAC near its narrowest point and where it displayed its greatest southward velocity (~29°S), and allowed to drift for 145.5 km (76.4 nautical miles [nm]) southward with the current until the point at which the current separated from the continental shelf downstream (~30.5°S; Figure 1); (b) an east–west (offshore–onshore) transect in Tasman Sea waters below the EAC separation zone at 32.2°S 153–155°E, hereafter referred to as non-EAC waters (Figure 1). At each sampling location, water column temperature and salinity were measured with a Seabird SBE911 CTD and water samples for microbiological and nutrient analysis were collected using 10 L Niskin bottles. Samples for 16S rRNA gene sequencing and shotgun metagenomics were collected from the surface (2–5 m) and the chlorophyll maximum layer (c_{max}), which varied from 20 to 70 m depending upon the depth of the water column. Seawater samples (2 L) were filtered upon collection onto 0.2 μm filters (Millipore). Filters were then snap frozen in liquid nitrogen and stored at −80°C. Dissolved inorganic nutrient analyses were carried out on board by CSIRO Oceans and Atmosphere from fresh samples taken directly from Niskin bottles, following standard protocols (Cowley et al., 1999).

2.1.2 | Oceanographic time-series

In addition to voyage samples, we collected time-series data from two Integrated Marine Observing System (IMOS) National Reference Stations (NRS) on the continental shelf of Australia's east coast, including at Port Hacking (PH) and Maria Island (MAI). The PH100 NRS (34.2°S, 151.2°E) is located three nm offshore and downstream of the EAC southerly separation zone near Sydney. Here, approximately 4 years of samples (April 2009–June 2013) were collected at near-monthly intervals from six depths (0, 10, 25, 50, 75 and 100 m; $n = 218$). The MAI NRS (42.6°S, 148.2°E) is located 4 nm offshore from MAI in the Tasman Sea, on the eastern coast of Tasmania. At MAI samples were collected approximately monthly for 1 year (July 2012–June 2013), at seven depths (0, 10, 20, 40, 50, 75 and 85 m; $n = 77$).

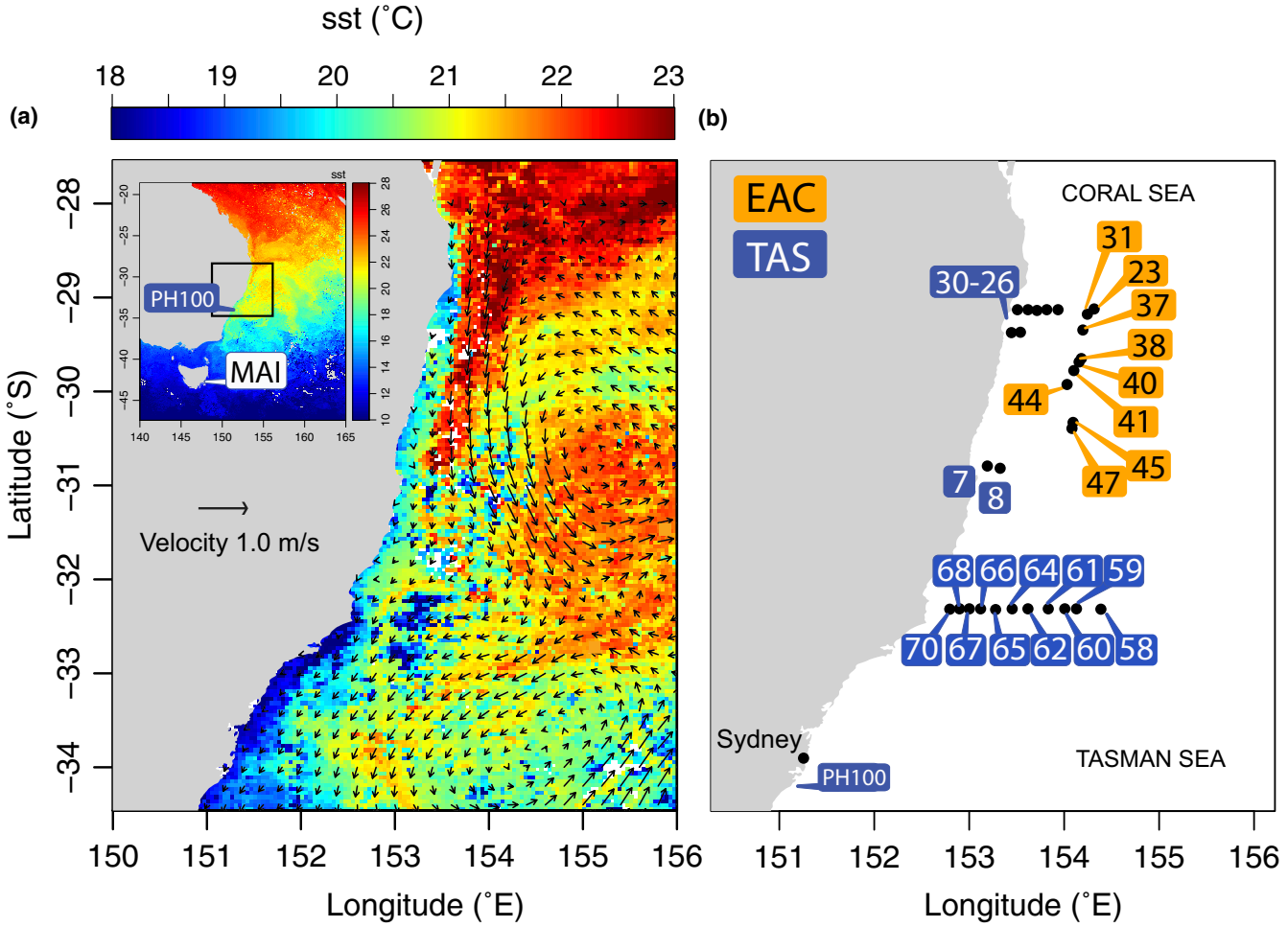

FIGURE 1 Maps displaying sites from which samples were collected during voyage ss2010_v09 of the RV Southern Surveyor, and locations of Integrated Marine Observing National Reference Stations, PH100 and Maria Island (MAI; inset). In the ocean colour map in (a) the East Australian Current (EAC) is characterized by increased sea surface temperature (°C), highlighted in dark red, and southward current velocities (black arrows), relative to the cooler Tasman Sea waters. In (b), stations labelled 31–47 within the EAC (orange) were completed during the Lagrangian drift. Stations in non-EAC waters (blue) were collected before (stations 7, 8, 26–30) and after (stations 58–70) the drift in the surrounding Tasman Sea. PH, Port Hacking [Colour figure can be viewed at wileyonlinelibrary.com]

At both stations, seawater samples for 16S rRNA gene sequencing (2 L) were collected using 5 L Niskin bottles mounted onto a hydrographic wire, and filtered after collection onto 0.2 μm Sterivex™ membrane filters (Millipore), frozen in liquid nitrogen then stored at −80°C. All metadata from the NRS time-series, including sea surface temperature, salinity, dissolved inorganic nutrients, zooplankton and phytoplankton counts and biomass, carbon and chlorophyll *a* concentrations were collected in accordance with the IMOS NRS sampling protocol (Lynch et al., 2008, 2014), are publicly available, and were extracted for this study from the IMOS Ocean Data portal (https://imos.aodn.org.au).

2.2 | Molecular and bioinformatic methods

2.2.1 | DNA extraction

Microbial DNA was extracted from filters using the PowerWater® DNA Isolation kit (MOBIO Laboratories, Inc.; now Qiagen) according to the manufacturer's directions. For samples collected from the IMOS NRSs from January 2012, DNA was extracted using a modified PowerWater® Sterivex™ DNA Isolation Kit (MOBIO Laboratories) protocol, including an initial 1 hr incubation of filter units on a horizontal vortex with 1.875 ml cell lysis buffer (5 mg/ml lysozyme, 200 mM $NaH_2PO_42H_2O$ and 200 mM Na_2HPO_4 final concentration) and 0.125 ml MT buffer (FastDNA™ Spin Kit for Soil; MP Biomedicals), followed by a phenol:chloroform extraction on cell lysate. The PowerWater® Sterivex™ DNA Isolation Kit protocol was then followed from the addition of ST4, according to the manufacturer's guidelines.

2.2.2 | 16S rRNA gene amplicon generation and sequencing and analysis

Partial 16S rRNA genes were amplified from microbial DNA using bacterial-specific primers 27F (5′-AGRGTTTGATCMTGGCTCAG-3′) and 519R (5′-GWATTACCGCGGCKGCTG-3′; Lane, 1991), and the

following reaction conditions: a single-step 30 cycle PCR using HotStarTaq® Plus Master Mix Kit (Qiagen) comprising 94°C initial denaturation (3 min), 28 cycles at 94°C (30 s), 53°C (40 s) and 72°C (1 min), with a final elongation step at 72°C (5 min). The resultant amplicons were purified using Ampure XP beads (Agencourt Bioscience Corporation) and sequenced at the Ramaciotti Centre for Genomics (University of New South Wales) using Roche 454 FLX Titanium instruments and reagents following the manufacturer's guidelines.

Amplicon quality control and analysis was implemented in Mothur (Schloss et al., 2009). Initial quality control of sequence data involved removal of short (<200 bp) sequences, removal of sequences with imperfect matches to the 5′ primer and the removal of sequences containing any unresolved (n) nucleotides. A 2% preclustering routine was used to remove potential errors in sequence data (Huse, Huber, Morrison, Sogin, & Welch, 2007). Sequences were aligned to the SILVA 119 database (Quast et al., 2013) and those that did not align in the appropriate zone were removed. Alignments were trimmed so that all sequences covered the entire alignment length. Potential chimeras were removed using the Chimera.slayer tool with the minsnp parameter set to 100. Samples were rarefied to 1,000 sequences to ensure even sampling effort across all samples, clustered into operational taxonomic units (OTUs) at 97% sequence identity using UCLUST (Edgar, 2010) and the taxonomic affiliation of representative sequences assigned according to the SILVA 119 database (Table S1).

2.2.3 | Metagenomic library preparation, sequencing and analysis

Metagenomic libraries were prepared from the same DNA stock that was used to generate 16S rRNA gene amplicons, using the Nextera® XT DNA Library Preparation protocol. Sequencing (250 bp paired end) was carried out on an Illumina HiSeq 2500 following the manufacturer's instructions (Ramaciotti Centre for Genomics). Adapters were removed from raw sequences with Trimmomatic v0.36 (Bolger, Lohse, & Usadel, 2014) and low-quality base pairs were trimmed with seqtk trimfq using default parameters (https://github.com/lh3/seqtk). Metagenomes were then assembled one sample at a time using MEGAHIT v1.0.2 (Li, Liu, Luo, Sadakane, & Lam, 2014; see Table S8 for various metagenome statistics). Gene prediction was performed using MetaGeneMark, on contigs >500 bp (Zhu, Lomsadze, & Borodovsky, 2010). To generate a reference gene catalogue, all predicted genes were clustered at 95% nucleotide identity using cd-hit (parameters: cd-hit-est -c 0.95 -T 12 -M 0 -G 0 -aS 0.9 -g 1 -r 1 -d 0; Li & Godzik, 2006). The relative abundance of each gene was then determined by mapping the filtered forward reads to genes in the catalogue using BLASTN (2.2.29+), retaining best hits of >60 nt or 60% alignment length. Functional and taxonomic annotations were assigned by BLASTN in comparison to the TARA Oceans Microbial Reference Gene Catalogue (Sunagawa et al., 2015) and additional NCBI taxon information was extracted by comparison against nr (February 2017 release) using Diamond (Buchfink, Xie, & Huson, 2014).

2.3 | Statistical analyses

2.3.1 | Comparing EAC and non-EAC microbial assemblages

Assemblage composition based on 16S rRNA gene amplicon data

The PRIMER + PERMANOVA (Plymouth Routines in Multivariate Ecological Research; v7) statistical software package was used to determine significant differences between EAC and non-EAC microbial assemblages. A Bray–Curtis dissimilarity matrix was generated from square-root transformed amplicon sequencing OTU abundance data and relationships between samples visualized using non-metric multidimensional scaling (nMDS). The non-parametric permutation procedure analysis of similarity (ANOSIM) was used to test for significant differences within and between EAC and non-EAC microbial assemblage structure, and the homogeneity of within-group multivariate dispersion was tested using the PERMDISP metric. The contribution of OTUs to the observed dissimilarity between the a priori designated groups was calculated using the similarity percentages procedure. The power of environmental variables to explain patterns between assemblages were examined using distance-based linear modelling. Significant differences between EAC (n = 21) and non-EAC (n = 27) environmental parameters, including temperature, salinity, fluorescence, nitrate, phosphate and silicate, were determined using the Kruskal–Wallis one-way analysis of variance (df = 1), after all data failed the Shapiro–Wilk normality test.

Assemblage function based on metagenomic data

Metagenomic count data for annotated functional genes were analysed using DESeq2 (Love, Huber, & Anders, 2014) and gene abundance data were summarized at the level of KEGG functional orthologs (Kanehisa & Goto, 2000; KO numbers). The site by gene abundance table was converted to a Bray–Curtis dissimilarity matrix and the relationship between gene profiles at each site (EAC n = 16; non-EAC n = 12) was determined using nMDS within the vegan package in R (Dixon, 2003). Significant differences in abundance were reported for functional genes fit to a negative binomial distribution using the Wald test with adjusted $p < .05$ as implemented in DESeq2 (Love et al., 2014). An independent analysis was carried out with SUPER-FOCUS (Subsystem Profile by database reduction using FOCUS) using Diamond in fast mode against DB_98 (Silva, Green, Dutilh, & Edwards, 2015) and proportional abundance profiles for subsystems were analysed using STAMP (Parks, Tyson, Hugenholtz, & Beiko, 2014; v2.1.3).

2.3.2 | Revealing the impact of the EAC

Calculating an index of the EAC impact using SourceTracker

To identify when the EAC was acting as a source for microbial assemblages at the PH100 site, we used the SourceTracker algorithm (Knights et al., 2011). This software uses a Bayesian classification model together with Gibbs sampling to predict the proportion of taxa in a given sink sample that are derived from multiple known

source environments. Source tracking has been used previously to indirectly infer the transport of microbes in deep-sea currents (Wilkins et al., 2013). The PH100 NRS site ($n = 218$) was defined as a sink site. Possible source populations supplied to the SourceTracker algorithm included samples collected during the oceanographic research voyage (ss2010_v09; EAC source, $n = 21$; Tasman Sea source, $n = 27$), plus a further Tasman Sea source data set ($n = 77$) generated monthly over 1 year from seven depths at the MAI IMOS NRS. OTUs that were present in <5 samples were excluded, as these were not expected to provide useful source tracking information. Source proportion estimates were predicted with 100 burn-ins and 25 random restarts. We defined an index, EAC_m, which equals the relative contribution of the EAC source microbial assemblage to the temperate coastal microbial assemblage at PH100, as determined by SourceTracker. The statistical significance of variation in EAC_m at PH100 ($n = 218$) was determined using a Kruskal–Wallis test, including the Dunn's test for pairwise multiple comparisons using 'month' and 'depth' as factors.

Relating EAC_m to ecosystem parameters

The relationships between EAC_m and temperature, salinity, stratification, dissolved inorganic nutrients and bacterial OTUs ($n = 140$ variables), were assessed using the maximal information coefficient (MIC; Reshef et al., 2011). The minimum number of observations required for a variable to be included in the analysis was set to 60% to encompass as much of the data as possible despite some missing values for physical and chemical variables downloaded from the IMOS Ocean Data portal. After multiple testing correction ($q = 0.05$; Benjamini & Hochberg, 1995), a total of 50 variables were identified as being significantly ($p < .001$), linearly and nonlinearly correlated with EAC_m (Table S6). Pearson correlation was used to determine the relationship between EAC_m and several biotic indices collected concurrently at PH100 that were indicative of the state of the broader ecosystem at the time of sampling. These included flow cytometric counts of picophytoplankton (*Prochlorococcus*, *Synechococcus* and picoeukaryotes), chlorophyll *a* concentration, total carbon biomass and indices of phyto- and zooplankton community structure, including diversity, abundance, cell volume and ratios of diatoms:dinoflagellates and herbivorous:carnivorous copepods (Table S10).

Determining differences in estimated microbial genome sizes from sequence data

To test the hypothesis that microbes inhabiting the EAC may have smaller genome sizes than those inhabiting non-EAC waters, MicrobeCensus was used to estimate the average microbial genome size based on the analysis of 30 single copy marker genes present in the metagenomic assemblies (Nayfach & Pollard, 2015). In addition, the genome sizes of taxa that significantly correlated to EAC_m at PH100 were estimated based on the nearest available phylogenetic neighbour as determined by a local BLASTN of representative 16S rRNA gene sequences against the NCBI RefSeq Genome Database Release 76 (O'Leary et al., 2016) using default settings. Results were manually curated to remove and reanalyse best hits that did not represent whole genome sequences (see Table S7). Significant differences between predicted microbial genome sizes were determined using one-way ANOVA, with the Tukey's post hoc test, for (a) the EAC and non-EAC surface and cmax communities; and (b) taxa positively and negatively correlated with EAC_m at PH100.

3 | RESULTS

3.1 | Characterization of microbial assemblages inside and outside the EAC

3.1.1 | The EAC maintains a microbial signature that is distinct from surrounding temperate seawater

To address our hypothesis that the EAC acts as a physical driver for shifting microbial assemblage structure in temperate waters, we collected samples for microbial analysis during a Lagrangian drift inside the EAC, along with samples from surrounding Tasman Sea waters (ss2010_v09; Figure 1). The EAC was identified as a southward flowing current (0.8 ± 0.2 m/s at 21 m depth) in which temperature was significantly elevated compared with non-EAC waters (Kruskal–Wallis test, $H = 19.3$, $df = 1$, $p < .001$). Taxonomic marker gene analysis (16S rRNA gene) of microorganisms collected inside the EAC ($n = 21$) and in non-EAC waters ($n = 27$; Table S1) revealed distinct assemblages inhabiting each system (Figure S1; ANOSIM, non-EAC vs. EAC: Global R: .35, $p < .001$). Temperature, chlorophyll fluorescence and dissolved inorganic nutrients were identified as the environmental variables best explaining the dissimilarity in assemblage structure (Table S2). EAC waters were substantially enriched in OTUs belonging to the picocyanobacterial genus *Prochlorococcus*, the alphaproteobacterial SAR11 Surface 1 (but not *Candidatus* Pelagibacter ubique) and Surface 2 clades, as well as the ultra-micro actinobacterial clade *Candidatus* Actinomarinidae (Figure S2; Table S3). Conversely, non-EAC waters harboured more sequences from the picocyanobacterial genus *Synechococcus*, chloroplasts (used here as indicators of eukaryotic phytoplankton), the alphaproteobacterial SAR11 *Candidatus* Pelagibacter and copiotrophic bacterial groups including the alphaproteobacterial *Roseobacter* and *Rhodobacter* clades, and members of the Bacteroidetes (Figure S2; Table S3).

The distinct microbial assemblage inside the EAC consistently displayed one of three tightly grouped assemblage states, one of which consisted of all samples from the EAC cmax, and shared a within-group pairwise Bray–Curtis similarity of 62.5%, despite being sampled over variable depths (Figure S1; PERMDISP, Table S9). The two other assemblage states consisted of surface samples collected at various positions along the Lagrangian drift, with average within-group pairwise Bray–Curtis similarities of 63.28% and 70.17% (Figure S1; PERMDISP, Table S9). Each state was defined primarily on the ratio of the cyanobacterial, actinobacterial and SAR11 ecotypes that dominated the EAC assemblage (Table S3). Despite the occurrence of three distinct assemblage states inside the EAC, samples collected hours apart were not more similar to each other than

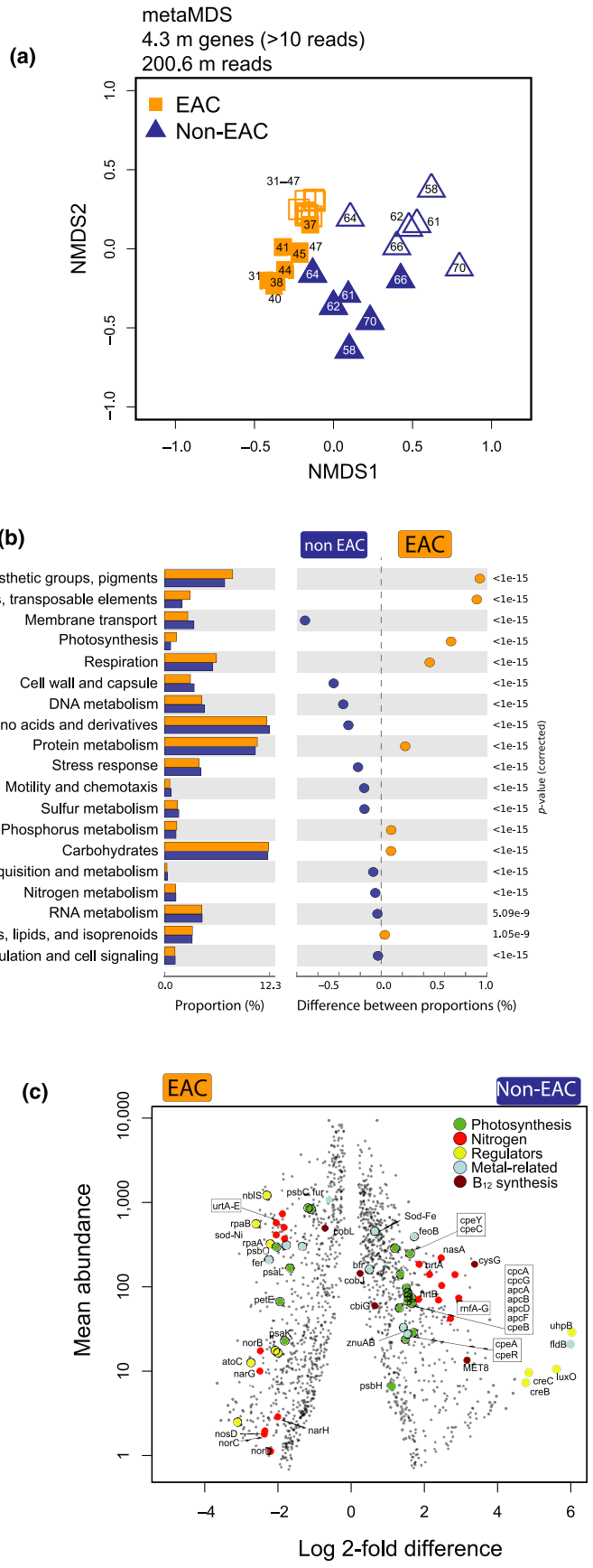

FIGURE 2 Metagenomic analyses revealed differences in the metabolic capacity of microbial assemblages collected inside the East Australian Current (EAC; $n = 16$) and in adjacent non-EAC waters ($n = 12$). (a) Non-metric multidimensional scaling plot highlighting clustering of the metabolic potential of microbial assemblages inside (orange squares, closed = surface, open = chlorophyll maximum) versus outside (blue triangles, closed = surface, open = chlorophyll maximum) the EAC. Numbers represent the station numbers from Figure 1b. In (b), significant proportional differential abundances between key metabolic subsystems in EAC and non-EAC waters are shown. (c) Mean abundances of individual genes demonstrating significant differential abundances greater than a log 2-fold change in EAC and non-EAC metagenomes [Colour figure can be viewed at wileyonlinelibrary.com]

to those sampled days apart, indicating that microbial community composition was maintained throughout the course of the drift (Figure S1). Indeed, the surface sample collected at the end of the drift was more similar to the surface sample collected 145 km to its north at the beginning of the drift, than any other sample. Hence, the EAC provided a strongly selective, stable habitat for the efficient transport of a coherent microbial assemblage across large distances.

3.1.2 | Comparison of microbial functional profiles using metagenomic analysis

Metagenomic analysis of representative EAC (n = 16) and non-EAC (n = 12) samples demonstrated significant differences in the metabolic capacity of EAC and non-EAC microbial assemblages (Figure 2a). On the one hand, the EAC metagenomes were enriched in metabolic subsystems related to cyanobacterial photosynthesis, prophage and transposable elements relating to cyanophage, cofactors and secondary metabolism, and fatty acid and lipid transport and metabolism (Figure 2b; Table S5). On the other hand, a greater proportion of subsystems associated with DNA metabolism, membrane transport and signal transduction mechanisms, transcription and flagella assembly and cell motility were detected in non-EAC assemblages (Figure 2b).

The differential abundances of individual genes revealed further differences in the metabolic adaptations of microbial assemblages inside and outside the EAC. In total, we identified 915 genes that were overrepresented in the EAC, and 1822 genes that were overrepresented in the non-EAC metagenomes (Figure 2c; Table S4). Consistent with the observed taxonomic shifts between the two systems, specific genes encoding the phycobilisome components allophycocyanin and phycoerythrin associated with *Synechococcus* were enriched in non-EAC waters (*apcABDF*, K02092-K02097 and *cpeABCD*, K05376-K03586, respectively). Additionally, genes involved in the synthesis of vitamin B_{12} required by eukaryotic phytoplankton for growth (*cob* genes, K05934, K02189, K00595, K02233), and the haeme-like prosthetic group siroheme critical for sulphur and nitrogen cycling in eukaryotic phytoplankton (*cysG* and *MET8*, K02302, K02304; Tripathy, Sherameti, & Oelmüller, 2010), were significantly elevated in the non-EAC metagenomes (Figure 2c; Table S4). Meanwhile, rhodopsin-related proteins, indicative of photoheterotrophy, were elevated in EAC metagenomes (Table S4). Moreover, the relative proportions of genes involved in the cycling of nitrogen indicated key differences in nitrogen utilization and availability, with genes involved in denitrification and nitrification (*narG* and *narH*, K00370, K00371) and the reduction of hydroxylamine to nitrite (*hao*, K10535), more prevalent within the EAC. In addition, genes for cyanobacterial nitrogen assimilation, including urease subunits and amino acid transporters, were also enriched in the EAC (Figure 2c). In contrast, genes encoding the small and large subunits of the nitrite reductase (NADH) enzyme, genes involved in dissimilatory nitrate reduction to ammonia (*nirB* and *nirD*, K00362, K00363), and the reduction of nitrite to nitric oxide (*nirK*, K00368), were elevated in non-EAC assemblages (Figure 2c; Table S4).

3.2 | Impacts of the EAC on a temperate coastal environment

3.2.1 | Source tracking the EAC at a coastal time-series site

To investigate how transport of the distinct EAC microbial assemblage impacts temperate regions, we used the SourceTracker algorithm to estimate the proportion of EAC-derived taxonomic marker genes (EAC_m) in samples collected at a temperate ocean time-series monitoring station (PH100) downstream of the EAC extension in the Tasman Sea. We identified a highly seasonal signature of EAC_m at PH100 (Kruskal–Wallis test, H = 90.3, df = 11, $p < .001$, n = 218), whereby average EAC_m contributed approximately 20%, but up to 60%, to the microbial community composition in late Austral summer and autumn months (February–June; Figure 3a). In contrast, during the Austral spring EAC_m was near zero, indicating that the microbial community composition during this season was not influenced by the EAC (September–November; Figure 3a). When grouped by sampling depth as opposed to month, EAC_m influence was most apparent in the top 50 m of the water column, but had little impact on microbial community composition in the bottom waters, 100m below the surface (Figure 3b; Kruskal–Wallis and Dunn's test; $H = 11.9$, $df = 5$, $p < .05$, $n = 218$).

3.2.2 | Ecosystem variables correlate with EAC_m

To identify potential relationships between EAC_m and physical, chemical and biological variables, we calculated the MIC between all variable pairs for the time-series observations at PH100. Using this approach, EAC_m was found to be positively correlated with temperature along with the relative abundance of a range of oligotrophic microbes, including *Prochlorococcus*, numerous OTUs from the alphaproteobacterial OCS116 and SAR11 Surface 1, 2 and 3 clades, gammaproteobacterial OM60, SAR406 and SAR324 clades (Figure 4; Table S6). On the other hand, EAC_m was negatively correlated with the inorganic nutrients nitrate and silicate, and a number of generally copiotrophic microbial taxa. These taxa include the Flavobacteria, such as *Polaribacter*, *Formosa* and the NS2 and NS4 marine clades, the gammaproteobacterial *Oceanospirillales* and K189A clades and the betaproteobacterial methylotrophic OM43 clade (Figure 4; Table S6). A number of taxa, including the SAR86, SAR11 and SAR92 clades, contained multiple distinct OTUs that displayed either positive or negative correlations to EAC_m, suggesting strain or ecotype transitions within these lineages (Figure 4; Table S6).

Importantly, EAC_m was also significantly correlated (Pearson, $p < .005$) with a number of independently derived quantitative indices reflective of the ecological state of the water column at PH100, including measures of phyto- and zooplankton composition and biomass (Figure 5; Figure S3; Table S10). Flow cytometry data provided quantitative support to the molecular observations that EAC_m was significantly positively correlated with *Prochlorococcus* abundance. Significant negative correlations were observed between EAC_m

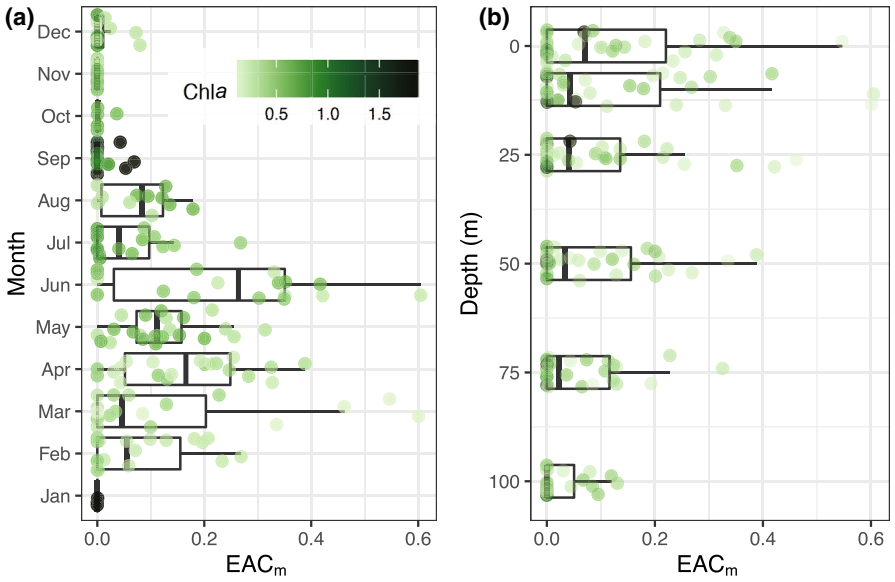

FIGURE 3 Source tracking of microbial assemblages at the PH100 time-series station near the East Australian Current (EAC) separation point reveals a strong seasonal influence of the EAC in temperate Tasman Sea waters. The green colour of each point is scaled to chlorophyll *a* concentration (Chla; inset). The microbial impact of the EAC (EACm) over approximately 4 years is shown integrated by month (January–December) in (a) and by depth in (b) at the PH100 station. PH, Port Hacking [Colour figure can be viewed at wileyonlinelibrary.com]

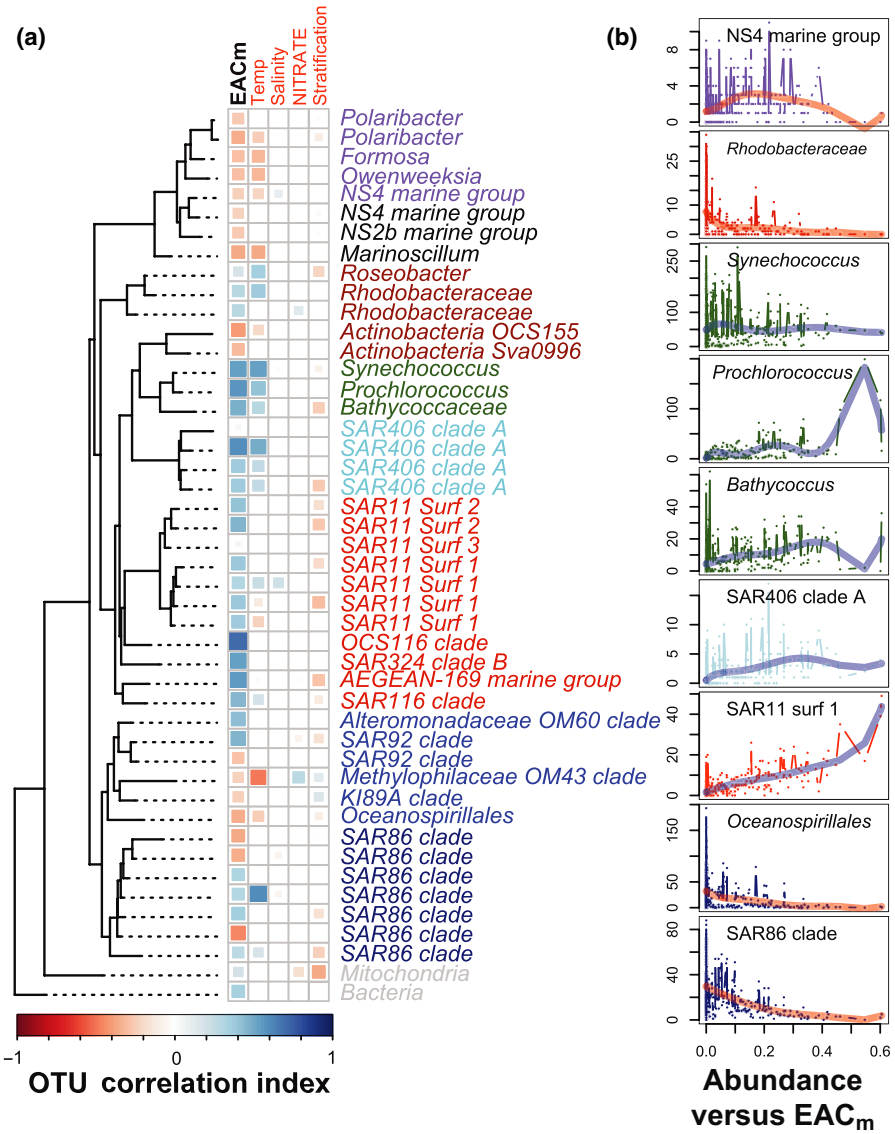

FIGURE 4 Significant linear correlations between EAC$_m$, environmental parameters, and specific OTUs from PH100 (a), as determined by the maximal information coefficient (OTU correlation index; $p < .001$; $q = 0.05$), and (b) the relationship between OTU read abundance (*y*-axis) and increasing EAC$_m$ (*x*-axis) across all PH100 sampling points ($n = 218$). In (a), the phylogenetic relatedness of OTUs are shown in a consensus phylogenetic tree. Representative 16S rRNA gene sequences from each OTU were aligned with MUSCLE (Edgar, 2004) and trees constructed using neighbour-joining and maximum-likelihood methods (Guindon et al., 2010; including JK correction and a GTR model). EAC, East Australian Current; EAC$_m$, microbial impact of the EAC; OTUs, operational taxonomic units; PH, Port Hacking [Colour figure can be viewed at wileyonlinelibrary.com]

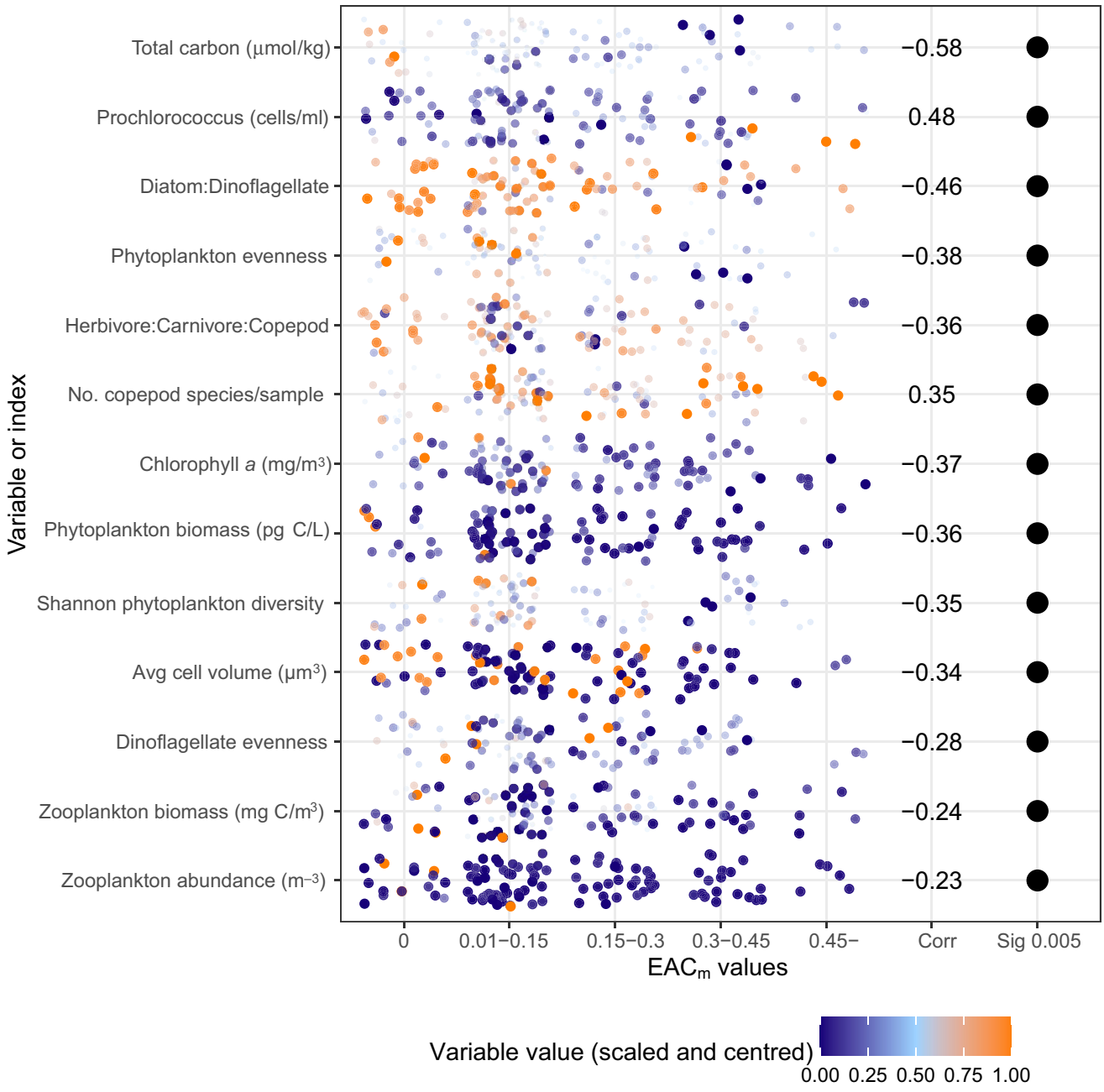

FIGURE 5 Significant relationships ($p < .005$) between EAC_m and ecosystem bioindicators from PH100. Values for indices were scaled and centred to enable plotting on a common scale and points were jittered to avoid overplotting caused by multiple discrete values of EAC_m. The Pearson correlation coefficient (corr) is provided for each variable and regression plots are provided in the Supporting Information (Figure S3). EAC, East Australian Current; EAC_m, microbial impact of the EAC; PH, Port Hacking

and phytoplankton specific indices including chlorophyll *a* concentration, phytoplankton carbon biomass, phytoplankton diversity, average phytoplankton cell volume and the ratio of diatoms to dinoflagellates (reflecting that when EAC_m was high, diatom abundances were relatively low compared to dinoflagellates; Figure 5; Figure S3; Table S10). Furthermore, zooplankton abundance, biomass and trophic composition (ratio of herbivorous to carnivorous copepods species present) were also all negatively correlated with EAC_m. Finally, the total carbon content of the water column displayed the strongest negative correlation to EAC_m of all the variables tested (Figure 5; Figure S3; Table S10).

3.2.3 | The EAC impacts genome size in microbial assemblages

We sought to test whether microbial assemblages associated with warmer oligotrophic waters aligned to ecological theories suggesting

that organisms with a higher optimum thermal growth rate (i.e. tropically adapted strains) often maintain smaller genomes (Sabath, Ferrada, Barve, & Wagner, 2013; Sorensen, Dunivin, Tobin, & Shade, 2019). Firstly, based on metagenomic data we observed significant differences between the estimated average genome sizes of microbes inhabiting EAC and non-EAC surface waters (one-way ANOVA, $F = 4.1$, $df = 3$, $p < .05$; Figure S4). The mean microbial genome size in the surface waters of the EAC was estimated to be ~2.4 Mbp, compared to ~2.9 Mbp in non-EAC surface waters (Figure S4). The estimated genome size of the cmax assemblages were not significantly different, estimated at ~2.75 and ~2.5 Mbp in the EAC and non-EAC respectively (Figure S4). Next, based on genome size data from the NCBI RefSeq database (O'Leary et al., 2016), we found that organisms that positively correlated to EAC_m at PH100 had significantly smaller predicted genome sizes (mean ~2 Mbp; $n = 24$) than those that were negatively correlated with EAC_m (mean ~3 Mbp; $n = 17$; One-way ANOVA, $F = 4.1$, $df = 1$, $p < .05$; Table S7).

4 | DISCUSSION

4.1 | The EAC maintains a distinct microbial assemblage to the Tasman Sea

In each of the major ocean basins, WBCs facilitate the transport of warm, oligotrophic seawater from the topics to temperate latitudes. Recently, these currents have also been implicated in the poleward redistribution of tropically adapted flora and fauna, contributing to the establishment of novel community structures in temperate waters (Figueira & Booth, 2010; Kingsbury et al., 2020; Vergés et al., 2014). Here we reveal that the EAC hosts a distinct microbial assemblage structure that is transported into temperate latitudes of the Tasman Sea. Our results demonstrate the relative stability of the EAC microbial assemblage along a 145 km Lagrangian trajectory, whereby the taxonomic and functional characteristics of microorganisms inside the warm, oligotrophic habitat remained distinct from those outside the current. Our findings suggest effective poleward transport over the sampled temporal and spatial scales and demonstrate the seasonal impact of the EAC on microbial assemblage structure at a temperate coastal site downstream the southerly separation zone of the current. These results collectively support our hypothesis that WBCs facilitate the transport of tropically adapted microbial populations into temperate latitudes, thereby expanding previous observations of macrospecies poleward range shifts. These findings provide critical empirical evidence to support previously untested predictions from model simulations of microbial drift and dispersal in upper ocean currents, including, (a) that poleward flowing WBCs carry microbes that have provenances in much warmer water than where they are ultimately found; and (b) that through their advective capacity, WBCs can influence the process of microbial assembly in temperate waters (Doblin & van Sebille, 2016; Villarino et al., 2018). Therefore, as WBCs increase in strength and intensity due to global climate change (Wu et al., 2012), we propose that the microbiology and biogeochemistry of temperate waters will likely transition towards a more oligotrophic state, potentially representing a profound biotic shift at the base of the marine food web.

The warm EAC waters contained low ambient concentrations of dissolved inorganic nutrients and supported enriched relative abundances of *Prochlorococcus* and SAR11 Surface 1 clade, consistent with the observations of these lineages in predominantly tropical and subtropical marine waters (Brown et al., 2012; Johnson, 2006). The waters surrounding the EAC were cooler with relatively higher concentrations of dissolved nutrients, conditions that supported taxa more typical of copiotrophic or coastal environments, such as *Flavobacteria* and *Bacteroidetes*, as well as the SAR11 genus *Candidatus* Pelagibacter (Brown et al., 2012; Lauro et al., 2009; Mazard, Ostrowski, Partensky, & Scanlan, 2012; Moran et al., 2007). Accordingly, the functional profiles of assemblages inside and outside the EAC aligned closely with expectations from models of oligotrophic versus copiotrophic systems respectively (Lauro et al., 2009). For example, genome architecture is a key cellular feature that has been used to discriminate microbial trophic lifestyle strategies. Oligotrophs and copiotrophs each maintain gene-specific metabolic adaptations to nutrient conditions (e.g. different number and affinity of transporters), and oligotrophs are generally characterized by overall smaller genome sizes compared to copiotrophs (Giovannoni, Tripp, et al., 2005; Lauro et al., 2009; Swan et al., 2013). To this end, EAC assemblages displayed smaller estimated genome sizes and genomic signatures that revealed more reliance on scavenging nitrogen from a diverse range of inorganic and organic sources than those in non-EAC waters. In the relatively copiotrophic non-EAC waters, ammonia was an important nitrogen source and genomic traits typical of a copiotrophic lifestyle in marine bacteria (Lauro et al., 2009), such as diversity of membrane transport and signal transduction mechanisms, and genes for flagella assembly and cell motility, were significantly enriched. Collectively, these data support our hypothesis that the EAC harbours an oligotrophic microbial community, more consistent with tropical oceanic conditions than with that of the surrounding waters.

4.2 | The EAC changes the base of the food chain

After demonstrating the Lagrangian transport of stable surface microbial assemblages within the EAC, source tracking determined the proportion of microbes at PH100 that were likely contributed by the distinct EAC assemblage (EAC_m), which closely matched the known temporal patterns of physical EAC flow. That is, EAC_m was near zero when EAC flow was at its weakest during Austral winter and spring months, and peaked during the Austral autumn when the EAC transport was at its maximum (Godfrey, 1980; Hamon, Godfrey, & Greig, 1975; Ridgway & Godfrey, 1997). The signature of EAC_m was most apparent in the top 50 m of the water column, consistent with oceanographic observations demonstrating that the physical influence of the EAC on the continental shelf is strongest in surface waters (Ridgway & Godfrey, 1997).

In-line with our observation that microorganisms within the EAC metagenomes had significantly smaller predicted genome sizes than those in non-EAC waters, organisms that were positively correlated with the EAC_m index at PH100 also displayed significantly smaller predicted genome sizes. Microorganisms with small genome sizes likely also maintain small cell sizes as both traits are associated with adaptation to higher temperatures (Sorensen et al., 2019) and oligotrophic conditions (Bouvier, Del Giorgio, & Gasol, 2007; Giovannoni, Tripp, et al., 2005; Lauro et al., 2009). Consistent with this, EAC_m was negatively correlated with both nitrogen, a critical nutrient for building nucleic acid structures, and chlorophyll *a* biomass, a proxy for marine primary production indicative of larger celled eukaryotic phytoplankton. EAC_m was also significantly correlated with smaller average phytoplankton cell volumes and lower phytoplankton-derived carbon biomass. A transition towards smaller microbial cell sizes under warming conditions has previously been observed in ex situ experiments, in which Atlantic coastal seawater was incubated under different warming scenarios (Huete-Stauffer, Arandia-Gorostidi, Alonso-Sáez, & Morán, 2016), while decadal observations from the same sampling site have indicated mean microbial cell sizes decreasing ~1% per year as a consequence of seasonal warming (Morán et al., 2015). In addition, the relative contribution of small phytoplankton cells to total phytoplankton biomass has been shown to increase with increasing temperatures (Morán, López-Urrutia, Calvo-Díaz, & Li, 2010). Recent modelling also suggests that picophytoplankton niche partitioning occurs along a temperature gradient according to cell size, with increases in the abundances of small picocyanobacteria (*Prochlorococcus* and *Synechococcus*) anticipated in response to projected future climate change scenarios (Flombaum et al., 2020). Moreover, evidence from a short-term (10 month) microscopy-based study to the north of our site (~30°S, 153°E) suggests that temperate phytoplankton in the region transition from a diatom-dominated assemblage to one composed primarily of warm water-associated dinoflagellates and cyanobacterial *Trichodesmium* sp. when the EAC flow is strong (Armbrecht, Schaeffer, Roughan, & Armand, 2015). We also observed a decrease in the ratio of diatoms to dinoflagellates when EAC_m was high, and many organisms in our data set that were abundant in the absence of the EAC have been found to be associated with diatoms. These lineages play an active role in the breakdown of compounds derived from eukaryotic phytoplankton, and include the OM43 clade (Morris, Longnecker, & Giovannoni, 2006; Sekar, Fuchs, Amann, & Pernthaler, 2004), Flavobacteria (Fernández-Gómez et al., 2013; Klindworth et al., 2014; Teeling et al., 2012), the gammaproteobacterial SAR92 clade (Klindworth et al., 2014; Teeling et al., 2012) and NOR05/OM60 clades (Yan et al., 2009). Collectively, these observations indicate a shift towards small phytoplankton and small microbial cells as a consequence of climate change, and these traits could continue to reduce under further warming (Sheridan & Bickford, 2011) due to the influence of the EAC.

The transition in the dominant organisms associated with photic energy capture, away from larger eukaryotic chlorophyll *a*-containing organisms such as diatoms, towards smaller picocyanobacterial (e.g. *Prochlorococcus*) photoautotrophs and dinoflagellates, and proteorhodopsin containing photoheterotrophs such as SAR11 clades 1, 2 and 3 (Giovannoni, Bibbs, et al., 2005), SAR86 (Béjà, Spudich, Spudich, Leclerc, & DeLong, 2001), and SAR92 (Stingl, Desiderio, Cho, Vergin, & Giovannoni, 2007), coincides with a reduction in herbivorous copepods and total water column carbon concentration at our study site. Many of the small organisms associated with EAC_m possess a simplified genomic capacity for carbon metabolism (Sun et al., 2011), and their small size is likely to impact the efficiency of carbon transport to higher trophic levels (e.g. zooplankton) as well as the sinking velocity of carbon-rich particles (Bopp, Aumont, Cadule, Alvain, & Gehlen, 2005; Morán et al., 2015; Morán et al., 2010). The biological carbon pump, whereby CO_2 is removed from the atmosphere via photosynthesis and carbon is sequestered to the sediment in the form of sinking particles, is known to be sensitive

TABLE 1 Conceptual summary highlighting the key findings from the present study and the implications of the results as the EAC continues to strengthen and intensify within south-eastern Australia

Source of observation	Influence of the Tasman Sea	Influence of the EAC
Lagrangian sampling, EAC_m time-series correlations, and literature	Higher chlorophyll *a*, >diatoms	Lower chlorophyll *a*, >cyanobacteria, dinoflagellates
Community composition and metagenomic data, and EAC_m time-series correlations	Large cells, larger genomes	Small cells, smaller genomes
Metabolic potential within metagenomes	Copiotrophs, chemotaxis used to locate nutrients	Oligotrophs, limited genomic capacity to utilize nutrients
Inferred from taxonomic markers and metagenomes, and EAC_m time-series correlations	More effective carbon remineralization	Proteorhodopsin, alternate photic energy capture
Supposition based on literature and EAC_m time-series correlations	Greater total carbon, greater biomass, sinking particles, export production	Reduced total carbon, reduced biomass, reduced capacity to form sinking aggregates
Supposition based on literature and EAC_m time-series correlations	Grazing by zooplankton, efficient trophic transfer	Reduced zooplankton grazing, decreased trophic transfer

Abbreviation: EAC, East Australian Current.

to changes in whole ecosystem community structure (Bopp et al., 2005; Henson et al., 2019). Consequently, the transition we outline may result in a fundamental community shift at the base of the marine food web, with significant implications for higher trophic levels and carbon sequestration in temperate waters (Table 1).

4.3 | Expanding EAC-driven tropicalization

Dispersal forces such as ocean currents may considerably enhance organismal redistribution and climate-driven range extensions when they directionally align with the spatial gradient of thermal change (Garciá Molinos, Burrows, & Poloczanska, 2017). Such is the case with the oceanographic system of eastern Australia. The poleward flowing warm waters of the EAC interact with southerly Tasman Sea waters that have been warming at ~3–4 times the average global rate for the past few decades (Holbrook & Bindoff, 1997; Ridgway, 2007). Our data show that the EAC effectively redistributes tropical microbes to the leading 'cold' edge of their range, contributing to seasonal patterns in abundance downstream. Furthermore, the presence of these microbial assemblages is accompanied by transitions in phytoplankton and zooplankton biomass and community structure, indicating this WBC may drive shifts in trophic status at the base of the pelagic food web in temperate waters. Hence our observations here provide a new and significant link between climate change-driven shifting ocean physics, microbiology and ecosystem function. They also provide contextualization to reports of the poleward range expansion of macroscopic organisms in the region that have been attributed in part to the increasing strength of the EAC (Armbrecht et al., 2015; Figueira & Booth, 2010; Harris, Griffiths, Clementson, Lyne, & Van der Doe, 1991; Johnson et al., 2011; Kingsbury et al., 2020; Last et al., 2011; Ling et al., 2009). These shifts have had substantial implications for the ecology of temperate waters in the region (Vergés et al., 2014), resulting in cascading losses of taxonomic diversity (Johnson et al., 2011; Ling et al., 2009), and the generation of new communities comprising sympatric tropical and temperate species (Kingsbury et al., 2020). Ultimately, our findings complement and extend to the microbial domain evidence that the EAC has driven the tropicalization of temperate biotic assemblages. Fundamental shifts in trophic status at the base of the pelagic food web are unlikely to be constrained by local intervention, so identifying microbial assemblage structure should become part of the integrated science assessment framework (Dawson, Jackson, House, Prentice, & Mace, 2011) for identifying climate change impacts and informing restoration efforts for populations, habitats and ecosystems (Duarte et al., 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Sequence data used in this study are publicly available through the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA), under BioProject PRJNA385736. In addition, the final quality-controlled amplicon sequence data set in.fasta format, sequence taxonomic assignments and mapping file used for SourceTracker analyses, the metagenome reference gene catalogue and abundance profiles and Tables S1 and S4 are also available through Figshare at reference https://figshare.com/articles/Australias_Ocean_Microbiome_Products/5576332. IMOS NRS physical and chemical data are publicly available through the Ocean Data portal (https://imos.aodn.org.au).

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SUPPORTING INFORMATION

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

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