RESEARCH ARTICLE

Natural and anthropogenic climate variability shape assemblages of range-extending coral-reef fishes

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Abstract

Aim: Climate change is redistributing species globally, resulting in altered community structures and ecosystem functioning. The current paradigm is that species should track temperature isoclines along latitudinal and depth gradients to remain within their thermal niches. However, the many exceptions to this rule point to complex ecological and environmental processes often overlooked in statistical models predicting species redistributions. We tested the contributions of natural versus anthropogenic climate change to the long-term spatio-temporal dynamics of assemblages of range-shifting tropical fishes at the leading edge of redistribution fronts.

Location: East coast of Australia.

Taxon: Tropical coral-reef fishes.

Methods: We analysed 16 years (2003–2018) of tropical species occurrences at two temperate locations using traditional diversity metrics (richness, accumulation curves and β-diversity). We also quantified the role of primary environmental covariates and estimated species associations using joint species distribution models.

Results: We reveal that tropical species richness has increased in this temperate ecosystem over time. Furthermore, we show that the richness of tropical vagrant species increased with the sea-surface temperature experienced by both local vagrants and their putative source populations at the southern Great Barrier Reef, which accounted for 23.1% and 22.1% of the explained variance, respectively. We also detected a signal from El Niño-Southern Oscillation, as species turnover and richness peaked during the strong La Niña event of 2010–2011.

Main conclusions: While the increases in ocean temperature and strength of the surface ocean current due to anthropogenic climate change are gradually favouring the poleward redistribution of tropical species, natural climatic oscillations can have a strong additive effect by rapidly modifying the pool of incoming species and potentially disrupting local communities.

KEYWORDS
climate change, coral reefs, ENSO, global warming, marine fishes, range shifts, species distribution, temperate ecosystems, transient community dynamics, vagrants

1 | INTRODUCTION

Ongoing climate change is forcing the relocation of marine and terrestrial species globally, threatening to alter the structure and functioning of communities (Poloczanska et al., 2007, 2013; Strona & Bradshaw, 2018). Quantifying the mechanisms underlying these shifts aids conservation planners and resource managers aiming to mitigate the impacts of climate change (Pecl et al., 2017). The general paradigm is that species undergoing redistribution track isotherms along latitudinal or depth/altitudinal gradients to maintain specific thermal conditions to which they are adapted (Chen et al., 2011; Parmesan & Yohe, 2003; Poloczanska et al., 2013). However, this simplification can ignore important environmental and ecological mechanisms at the individual, population and community levels, which can reduce our ability to model and predict range shifts robustly (Burrows et al., 2019; Monaco, Nagelkerken, et al., 2020; Pinsky et al., 2013; Sunday et al., 2015; VanDerWal et al., 2012).

Along with human-mediated climate change, natural climatic oscillations also influence range dynamics of marine vertebrates and invertebrates globally (Harley & Paine, 2009; McLean et al., 2018; Pearce & Hutchins, 2009; Wilson et al., 2018). These include both global and regional climate systems that cycle semi-regularly over decadal (e.g. El Niño-Southern Oscillation, ENSO) or multi-decadal (e.g. Atlantic multidecadal oscillation) periodicities. These oscillations have profoundly modified the structure and functioning of marine communities in different oceans (e.g. South Pacific: Gaymer et al., 2010; North Atlantic: McLean et al., 2018). These effects depend both on the cycle phase and on region-specific patterns shown by the relevant physical drivers (Krokos et al., 2019; Redondo-Rodriguez et al., 2012). For instance, along the west coast of Australia, high values of the southern oscillation index indicating La Niña conditions have been associated with enhanced advective transport and warmer sea-surface temperatures, resulting in higher rates of recruitment of tropical fishes into temperate locations than during neutral or El Niño conditions (Pearce & Hutchins, 2009; Wilson et al., 2018). In contrast, along the north-eastern coast of Australia, estimates of fish recruitment were higher during the opposite ENSO phase (El Niño) (Cheal et al., 2007). Therefore, capturing the mechanisms driving dynamics of communities shifting their ranges requires quantifying the contributions of both natural climatic oscillations and the long-term forcing of climate change, with explicit consideration of oceanographic characteristics in the wider region (Krokos et al., 2019).

The reshuffling of communities in response to physical drivers is complicated by the ecological context in which it occurs, including physiological and behavioural adjustments by organisms to cope with novel conditions (Kearney & Porter, 2006; Nagelkerken & Munday, 2016), as well as positive or negative interactions among species (HilleRisLambers et al., 2013; Nagelkerken et al., 2020). At their range limit, distributional shifts might be impeded by local food availability, competitors, predators (Figueira et al., 2019) and parasites, or else expansions could benefit from enhanced conditions provided by novel resources, reduced predation pressure and facilitation by habitat provisioning (Holt & Barfield, 2009; Monaco, Bradshaw, et al., 2020; Smith et al., 2018).
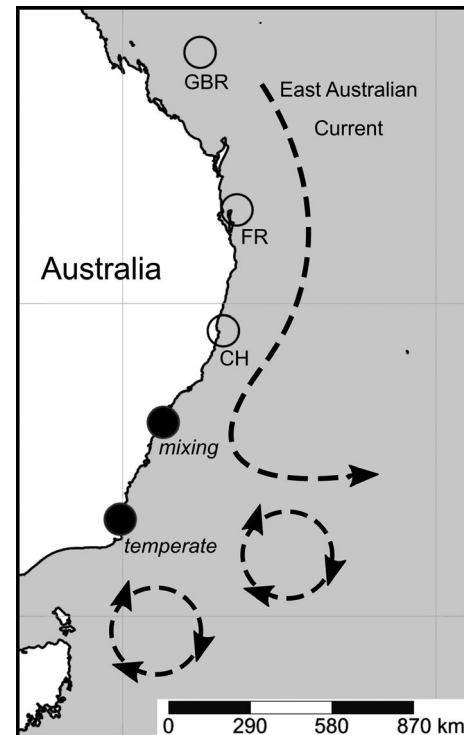

FIGURE 1 East coast of Australia and study locations. The filled circles mark the *mixing* and *temperate* locations monitored during the study, while the clear circles show the three putative source locations of tropical fishes (CH, Coffs Harbour; FR, Flinders Reef; GBR, southern Great Barrier Reef). The dashed lines represent the southward East Australian current and associated eddies. We used *SimpleMappr* (simplemappr.net) to draw the map

While there are many examples demonstrating mechanisms for redistribution of model species, few studies have effectively upscaled these processes to the assemblage level and in the context of climate change (Burrows et al., 2019; Singer et al., 2016; Urban et al., 2016). Joint species distribution models are emerging as promising approaches that integrate responses of multiple species to abiotic environmental drivers to understand and predict community dynamics (Ovaskainen et al., 2017; Pollock et al., 2014; Thorson et al., 2015). These models might be particularly useful for characterizing range-shift dynamics of assemblages whose species have different dispersal potential, physiological sensitivities and demographic responses, because such models can explicitly account for these processes (Ovaskainen et al., 2017).

Because of high rates of seawater warming along the southeastern coast of Australia, and an intensified East Australian Current (Ridgway, 2007), the temperate part of this region has received many tropical and sub-tropical marine species over the last few decades, most notably fishes, which have been documented through dedicated surveys (Booth et al., 2007; Fowler et al., 2017; Last et al., 2011) (Figure 1). Although most of these species have yet to establish breeding populations, observed trends and model simulations indicate that the full range of annual temperatures will become suitable for at least some of them in the next decade (Fowler et al., 2017; Monaco, Nagelkerken, et al., 2020). Currently, predictions integrating species

responses for entire assemblages are not available; therefore, it is unclear how community structures of range-extending tropical species are re-shaping at their leading edges. Regional variability in rates of warming, dynamic coastal eddies and broad-scale oceanographic cycles (e.g. ENSO) make south-eastern Australia an excellent model system to examine the mechanistic role of multiple abiotic and biotic drivers on the redistribution of marine species.

We designed a three-phase analysis of the redistribution processes of tropical fish assemblages in temperate south-eastern Australia using a 16-year dataset documenting coral reef-fish occurrences at two temperate locations (Booth et al., 2007, 2018). We first measured the rates of change in species richness, cumulative number of species across the period of the study (Ugland et al., 2003) and assemblage-resemblance analyses by quantifying temporal β-diversity and its components: that is, similarity, species replacement, and differences in species richness (Legendre, 2014; Podani & Schmera, 2011). Assuming a gradual, poleward redistribution forced by human-induced climate change, we hypothesized a linear increase in tropical-fish species richness over time at the leading edges, and a total number of tropical-fish species inversely proportional to latitude. Regarding β-diversity, we expected a gradual reduction in similarity between the tropical-fish assemblages monitored over time, relative to the first-year reference assemblage. Second, we quantified the contribution of physical drivers to this redistribution process using assemblage-level joint species distribution models. Based on prior knowledge (Booth et al., 2007; Monaco, Nagelkerken, et al., 2020; Pearce et al., 2016; Wilson et al., 2018), we tested the hypotheses that tropical species richness responds positively to sea-surface temperature (both experienced locally at the leading edge and by candidate tropical source populations), the strength of the East Australian Current and ENSO. The hypothesis that warm conditions at the source populations could favour recruitment at the temperate sites was suggested by research showing a positive effect of slight increases in temperature on the fertility of some tropical fishes (Pankhurst & Munday, 2011). Because information regarding the true source of the recruits was unavailable, we tested three candidate populations as the source. Third, after controlling for the species' joint responses to abiotic drivers, we examined species associations inferred from the model based on residual correlations (Ovaskainen et al., 2017). Based on the proximity to the potential source populations and the expected decrease in vagrancy/invasion towards the pole (Booth et al., 2011; Guo, 2014), we predicted that there would be more species associations among these vagrant species at the warmer equatorward locations compared with those in more temperate waters.

2 | MATERIALS AND METHODS

2.1 | Species occurrence records

We used data on coral-reef fish occurrence (i.e. presence/absence) collected at the temperate locations of Cabbage Tree Bay, Sydney (33° 48′ 00″ S, 151° 17′ 50″ E), and Bar Beach, Merimbula (36° 53′ 45″ S, 149° 55′ 26″ E) (Figure 1), as part of a long-term program to document species' range shifts (Booth et al., 2007). The habitat structure was similar between locations, characterized by shallow (< 5 m deep) rocky reefs with alternating patches of kelp, sessile filter feeders and bare rock (personal observation, D Booth). The presence of habitat-forming species has changed in some locations of this region due to warming (Vergés et al., 2014); however, while we did not monitor the cover density of these species formally, there was no apparent loss of kelp at either site. While Sydney is considered here as a temperate mixing zone (hereafter, *mixing location*), with regular recruitment of tropical and sub-tropical fishes and corals, Merimbula maintains a true-temperate condition (hereafter, *temperate location*) (Booth et al., 2018; Booth & Sear, 2018). We defined the species surveyed as tropical/sub-tropical if they breed within tropical coral-reef habitats, and their larvae show or have shown settlement into temperate-reef habitats as well (Feary et al., 2014).

Surveys were done by snorkeling using the roaming underwater visual census method (Beck et al., 2014), covering areas of ~1,000 m^2 at each location. These were done at least monthly between 2003 and 2018 (2017 at the *temperate* location) (Booth et al., 2007; Fowler et al., 2017). While other coastal locations have been surveyed as part of the long-term monitoring program, only Sydney and Merimbula have been sampled with sufficient regularity during the period of this study to provide data appropriate for our analyses. To analyse assemblage dynamics, we grouped the occurrence data by quarters of a year, and produced species × survey matrices for each location. To maintain a balanced sample size between locations, we worked with data from the first two quarters of each year, which would not bias conclusions because that is when most recruitment of tropical fishes occurs (Booth et al., 2007; Feary et al., 2014). In total, and including 3 years with only one quarter surveyed at the temperate location, the number of surveys was 32 and 26 for the *mixing* and *temperate* locations, respectively.

2.2 | Indices of diversity

To describe the change of tropical species diversity over time, we calculated species richness (i.e. number of species) and derived species accumulation curves (Ugland et al., 2003). To reveal the ecological phenomena underlying the changes in species diversity, we estimated β-diversity and its components (i.e. similarity, replacement and richness differences between years) (Legendre, 2014; Podani & Schmera, 2011). We used the *R* packages `vegan` (Oksanen et al., 2019) to calculate species richness and accumulation, and `adespatial` (Dray et al., 2020) to estimate β-diversity and its components. For the latter, we worked with Jaccard-based Podani indices suitable for comparing presence–absence data (Podani & Schmera, 2011). Briefly, the components of β-diversity calculated for pairs of surveys are defined as follows: similarity (*Sim*) is the number of shared species between surveys divided by the total; relative species replacement (*Repl*) is the maximum fraction of species turnover that is equally shared by the two surveys, divided by total number of species; and relative richness

difference (*RichDiff*) is the absolute difference in number of species between surveys, divided by the total. We illustrate the temporal evolution of β-diversity using ternary plots that depict *Sim*, *Repl* and *RichDiff* for each year compared to the reference (2003), that is, the first year of our surveys (Legendre, 2014). This is possible because the Podani family of diversity indices (*Sim*, *Repl* and *RichDiff*) sum to 1, with *Repl* + *RichDiff* = 1 – *Sim* (Podani & Schmera, 2011).

2.3 | Joint species distribution models

Joint species distribution models rely on standard assemblage and environmental data collected across space and time to quantify the probability of species co-occurrences, accounting for shared environmental responses and correlations among species (Ovaskainen et al., 2017; Pollock et al., 2014; Thorson et al., 2015). The ability of joint species distribution models to capture associations among species, and the advances in computational capacity to handle demanding hierarchical model structures, have popularized their application in community ecology (e.g. Schliep et al., 2018; Wilkinson et al., 2019).

Using the *R* package HMSC (hierarchical modelling of species communities) by Ovaskainen et al. (2017), we modelled species occurrence y_{ij} (i^{th} sampling event of the jth species) based on linear predictors L_{ij} and variance σ_j^2, and assuming a binomial distribution with a probit link function: $y_{ij} \sim \text{probit}(L_{ij}, \sigma_j^2)$. The linear predictors result from the additive effects of fixed L_{ij}^F and random L_{ij}^R terms, such that $L_{ij} = L_{ij}^F + L_{ij}^R$.

The fixed effects are quantified as a multiple regression model with χ_{ik} environmental covariates (k), the regression parameters that specify species-specific responses β_{jk} and an intercept of 1 for scaled covariates: $L_{ij}^F = \sum_k x_{ik} \beta_{jk}$. The parameter β_{jk} therefore captures the species' realized niche, which is modelled as a Normal distribution with expected mean μ_{jk} and variance given by a variance–covariance matrix V, such that $\beta_{jk} \sim N(\mu_{jk}, V)$. Because redistributions can depend on species traits and phylogeny (see *Species traits and phylogeny* below) (Feary et al., 2014), we also included their expected linear effects on μ_{jk} (Abrego et al., 2017): $\mu_{jk} = \sum t_{jl} \gamma_{lk}$, where γ_{jl} is the value of trait l, and γ_{lk} represents the effect of trait l on the response to covariate k.

The random effects ($L_{ij}^R = \varepsilon_i$) represent the variation in species occurrence and co-occurrence after controlling for environmental covariates (Ovaskainen et al., 2016), and are ascribed to location ε_i^S and year ε_i^Y. We modelled these assuming a Normal distribution, a mean of zero and a residual species-to-species covariance matrix Ω, where $\varepsilon_i \sim N(0, \Omega)$. The sub-diagonal row of the association matrix ($\Omega_{j_1 j_2}$) describes the covariation among species j_1 and j_2. We calculated the residual species-to-species associations by a correlation matrix R, where $R_{j_1 j_2} = \Omega_{j_1 j_2} / \sqrt{\Omega_{j_1 j_1} \Omega_{j_2 j_2}}$, parameterized using the latent variable approach (Ovaskainen et al., 2016) — a technique that can simplify the estimation of associations between species pairs in rich communities. To infer the extent to which species were associated more or less often than expected by chance, we focused on the species associations derived from the random effect of year, and ignored the location effect. We did this because we assumed that

the large-scale spatial variability in species co-occurrences would not result from realized interactions among individuals. Despite known swimming abilities of these larvae (Leis & McCormick, 2003), we assumed vagrant fishes dispersed mostly passively via ocean currents at least until they moved onshore to temperate reefs (Feary et al., 2014). In contrast, species can effectively co-occur at particular locations over time, suggesting that the random variable *year* would provide more accurate information about possible ecological associations. Note that while active swimming ability of larvae might be relevant for local, on-shore transport, we do not expect this to influence the larger-scale variability in settlement examined here.

Following Ovaskainen et al. (2017), we used a Bayesian inference approach to parameterize the joint species distribution models. We used Markov chain-Monte Carlo to sample posterior distributions (chains = 4, iterations = 160,000, burn-in = 60,000). We fitted 1 null and 20 candidate models that included all combinations of four covariates (see *Environmental covariates* below) and four traits specified separately (see *Species traits and phylogeny* below). To rank the models based on cross-validation performance, we used the coefficient of discrimination $Tjur^2$, and the area under the receiver-operating characteristic curve (AUC). $Tjur^2$ is calculated as the difference between average fitted values for successes and failures, and ranges between 0 and 1 (Tjur, 2009).

2.4 | Environmental covariates

Based on previous knowledge (Booth et al., 2018; Fig ueira & Booth, 2010), we considered the following environmental covariates for each year of the 16-year dataset: (1) sea-surface temperature experienced by fishes at the *mixing* and *temperate* locations (SST), (2) sea level (SL) as a measure of the strength of the East Australian Current (Pearce et al., 2016), (3) southern oscillation index (SOI) as a measure of ENSO and (4) sea-surface temperature potentially experienced by parent fish of vagrants at three candidate locations (Coffs Harbour, SST_{CH} [30° 52′ 41.80″ S, 153° 12′ 47.00″ E]; Flinders Reef, SST_{FR} [27° 00′ 53.54″ S, 153° 38′ 48.00″ E]; southern Great Barrier Reef, SST_{GBR} [21° 58′ 54.62″ S, 152° 28′ 23.62″ E]). Because we lacked information on the exact larval source location(s), and this can vary as a function of species' pelagic larval duration and variability in ocean-circulation patterns, we chose these last three regions to represent an area encompassing the putative parent source populations (Feary et al., 2014). Changes in ocean productivity have little influence on the dynamics of these fishes (Monaco, Nagelkerken, et al., 2020), so we excluded this potential driver from our analyses.

We downloaded satellite-derived (NOAA—polar-orbiting operational environmental satellites) estimates of SST from the Integrated Marine Observing System repositories (imos.org.au). We used 'skin' sea-surface temperature estimates (day–night composites) available daily at a horizontal resolution of 1.1 km. We extracted pixels 15 km offshore (with 10-km circular buffers) at the *mixing* location (33° 49′ 58.296″ S, 151° 23′ 53.88″ E), *temperate* location (36° 54′ 49.60″ S, 150° 02′

02.00″ E), Coffs Harbour, Flinders Reef, and the southern Great Barrier Reef. We grouped the environmental data by quarter to match the occurrence data, and used the 99th percentile in the joint species distribution models.

We downloaded data for sea level—a proxy for southward ocean surface current velocity and larval transport (Pearce & Hutchins, 2009)—from the Australian Bureau of Meteorology (bom.gov.au; accessed June 2019). We used records from the locations Fort Denison (33° 51′ 16.8″ S, 151° 13′ 32.8″ E) and Eden (37° 04′ 25.1″ S, 149° 54′ 27.9″ E), which are the closest stations within 20 km of our *mixing* and *temperate* locations, respectively. Data are available monthly and we used the maximum value per quarter in the models. We used the southern oscillation index (McBride & Nicholls, 1983) as a measure of the ENSO strength. This index is calculated based on the difference in atmospheric pressure recorded between Darwin and Tahiti. We downloaded monthly records available from the Bureau of Meteorology, and worked with quarterly maxima in our model runs. Because the ENSO cycle affects these tropical vagrants by altering climate change-related environmental variables (e.g. temperature, ocean circulation) (Wilson et al., 2018), their signals would not be completely decoupled in the analyses. However, the southern oscillation index, unlike other metrics of ENSO (e.g. multivariate ENSO index), is not calculated directly from these variables, which prevented collinearity in the models and allowed effective detection of their relative contributions to assemblage dynamics. All the environmental covariates were continuous variables, and we detected no autocorrelation between them (pairwise Pearson correlation tests: $r < 0.4$ in all cases).

2.5 | Species traits and phylogeny

The joint species distribution models accounted for non-independent responses of species owing to trait similarities and phylogenetic relatedness. We used species trait data (Table S1) sourced from Feary et al. (2014): maximum total body length (*MaxLength*), latitudinal distribution (*LatDist*), pelagic larval duration (*PLD*) and coral habitat dependence (*CoralDep*). We used *FishBase* (Froese & Pauly, 2019) to extract species trophic level (*Troph*). Although the fish diet records in this repository are often life stage-specific, we used data for adults when juvenile information was unavailable. We controlled for phylogenetic relatedness between species in the joint species distribution models using phylogenetic taxonomy data curated by the National Center for Biotechnology Information (Federhen, 2011).

3 | RESULTS

3.1 | Species diversity dynamics

Species richness increased over time at the *mixing* location (linear model vs. intercept-only model: evidence ratio = 1.56, effect size $f^2 = 0.11$; Figure 2a) and at the *temperate* location (linear model vs.
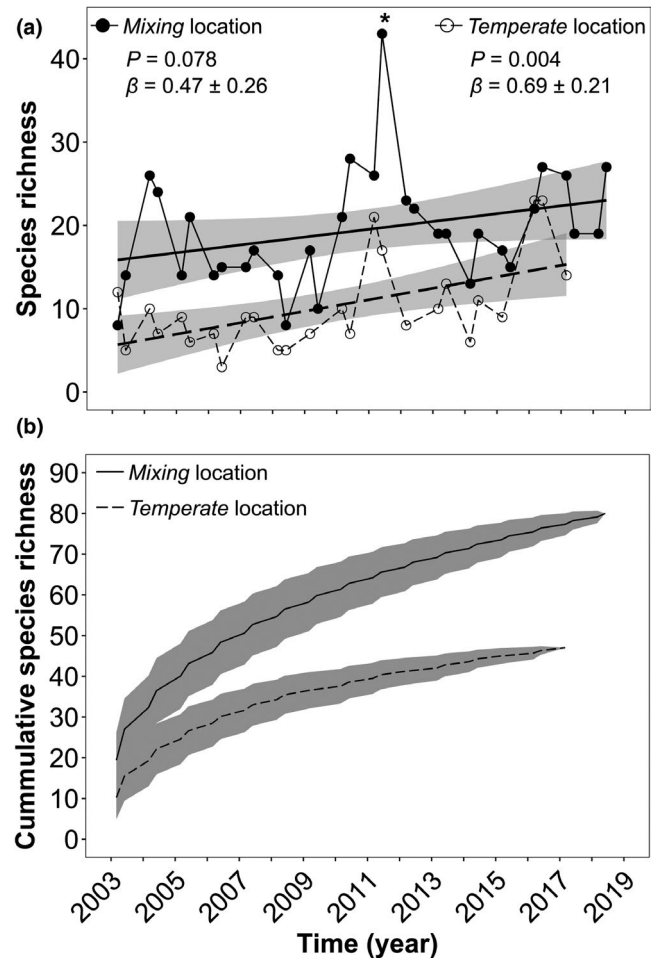

FIGURE 2 Tropical vagrant fish-assemblage dynamics for *mixing* and *temperate* locations surveyed between 2003 and 2018/2017 (*mixing/temperate* locations). (a) Species richness quantified (nearly) twice yearly for the *mixing* and *temperate* locations. The fitted linear regression line for species richness as a function of time (± 95% confidence interval) is provided. *highlights 2011 with strong ENSO influence. (b) The estimated cumulative number of tropical species that settled at the two locations over time

intercept-only model: evidence ratio = 30.25, effect size $f^2 = 0.44$; Figure 2a). Despite this slightly faster rate of colonization at the *temperate* location (Figure 2a), the cumulative species richness curves show that the *mixing* location received 65% more tropical species by 2017 than the *temperate* location (Figure 2b). An asymptotic model (Lomolino, 2000) fitted to the species accumulation curves further indicated that at current rates, the model-projected asymptote for the *mixing* location would reach 229 fish species, versus 96 at the *temperate* location (from an initial 8 and 12 species in 2003, respectively).

The temporal dynamics of species diversity indices were dominated by fluctuations in two axes of the β-diversity components: species replacement (*Repl*) and species richness differences (*RichDiff*) (Figure 3). The relative contributions of *Repl* and *RichDiff* varied between 0 and 0.7, with no one process overwhelming the other (mean ± 1 *SD*, *mixing* location: *Repl* = 0.22 ± 0.14,

RichDiff = 0.32 ± 0.17; *temperate* location: *Repl* = 0.37 ± 0.18, *RichDiff* = 0.27 ± 0.19). The balance between *Repl* and *RichDiff* further translated to relatively stable values of species similarity (*Sim*) over time for both the *mixing* and *temperate* locations (linear regression, effect of time: *mixing* location: $p = 0.998$; *temperate* location: $p = 0.404$). The variability of *Sim* was also lower than that of *Repl* and *RichDiff* (mean ± 1 *SD*, *mixing* location: *Sim* = 0.45 ± 0.08; *temperate* location: *Sim* = 0.36 ± 0.09). At both locations, we observed the largest departure from the average *Sim* values during the La Niña period in 2010–2011 (Figure 3). At the *mixing* location, this was accompanied by an increase in *RichDiff* and a decrease in *Repl*, while at the *temperate* location these indices were more stable (Figure 3).

To examine anomalies in assemblage composition across time, we ran permutation tests of the yearly contribution to *β*-diversity (i.e. uniqueness of an assemblage) (Legendre & De Cáceres, 2013), revealing that only for the *mixing* location, the 2011 fish-assemblage structure differed from other years (permutation test: 100,000

FIGURE 3 Ternary plots of the relationships between the reference year 2003 and each subsequent sampling year (*mixing* location: 15 contrasts; *temperate* location: 14 contrasts) for the (a) *mixing* and (b) *temperate* locations. The points depict relative species similarity, replacement and richness difference. The first and last contrasts are shown in blue and red, respectively. The width of lines and points increase with time. *highlights 2011 with strong ENSO influence [Colour figure can be viewed at wileyonlinelibrary.com]

permutations, Holm correction, $p = 0.041$). During the 2010–2011 La Niña, we recorded 34 and 25 new species at the *mixing* and *temperate* sites, respectively. While some of these species were not observed again afterwards (*mixing* location *n* = 17 [70.8% of total species richness at the respective site], *temperate* location *n* = 8 [42.1%]), others reoccurred at least once (*mixing* site *n* = 7 [29.2%], *temperate* location *n* = 11 [57.9%]) between 2011 and 2019.

3.2 | Joint species distribution model selection

The joint species distribution model with the highest descriptive power (i.e. highest mean $Tjur^2$; Table 1, Table S2) was the model including all four environmental covariates: sea-surface temperatures at the *mixing* and *temperate* locations, sea-surface temperature experienced by the potential source populations at the southern Great Barrier Reef, sea level, and southern oscillation index. The models that considered the sea-surface temperature experienced by the alternative source populations of Coffs Harbour and Flinders Reef received less support (Table 1, Table S2). Model skill (AUC) also improved when models incorporated functional traits and accounted for phylogeny, especially when considering the species' latitudinal distribution (mean $Tjur^2$ = 0.193, mean AUC = 0.906) or their pelagic larval duration (mean $Tjur^2$ = 0.192, mean AUC = 0.899; Table 1, Table S2). The ability of the highest-ranked model to describe dynamics of individual species increased with species prevalence (i.e. frequency of occurrences across surveys) up to 31 observations (56.4% of maximum possible prevalence), and decreased thereafter (Fig. S1).

3.3 | Importance of environmental covariates and random variables

In the highest ranked joint species distribution model (Table 1), the total variance explained was primarily associated with environmental covariates (74.4% of total variance explained by the model) and, to a lesser extent, the random variables (25.6% of total variance explained by the model; Figure 4, S2). While changes in sea-surface temperature experienced by the potential source populations at the southern Great Barrier Reef accounted for 23.1% of this variance, sea-surface temperatures at the *mixing* and *temperate* locations, the southern oscillation index and sea level were responsible for explaining 22.1, 16.9 and 12.3% of the variance, respectively. The importance of these predictors was also reflected by the number of species that responded to them. For instance, while 32 species were positively affected by the sea-surface temperature at their potential source populations (the main driver), only one species responded to sea level (Fig. S3). Models that included the effects of sea-surface temperature experienced by the potential source populations at either Flinders Reef or Coffs Harbour received little support (Table S2). The five top-ranked models (Table 1) revealed that the effects of these covariates favoured certain traits. In particular, warmer local sea-surface temperatures were associated with wider latitudinal distributions (probability that first and
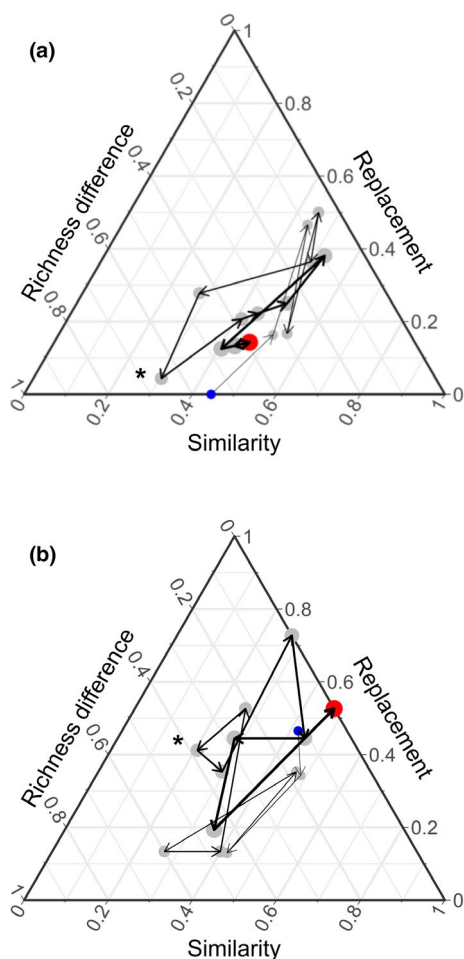
TABLE 1 Five top-ranked joint species distribution models arranged based on the coefficient of discrimination averaged across species (mean $Tjur^2$)

Model rank	Covariates	Random	Trait	Phylogeny	Sampling units	Species	mean $Tjur^2$	mean AUC
1	SST + SST$_{GBR}$ + SL + SOI	location + year	*LatDist*	Yes	56	81	0.193	0.906
2	SST + SST$_{GBR}$ + SL + SOI	location + year	*PLD*	Yes	56	68	0.192	0.899
3	SST + SST$_{GBR}$ + SL + SOI	location + year	None	No	56	91	0.181	0.911
4	SST + SST$_{GBR}$ + SL + SOI	location + year	*MaxLength*	Yes	56	86	0.180	0.902
5	SST + SST$_{GBR}$ + SL + SOI	location + year	*CoralDep*	Yes	56	91	0.179	0.908
37	Intercept-only	None	None	No	58	92	0	0.5

Note: SST, sea-surface temperature experienced by fishes at the mixing and temperate locations; SST$_{CH}$, SST$_{FR}$ and SST$_{GBR}$, sea-surface temperature experienced by potential parent fish of vagrants at Coffs Harbour, Flinders Reef and the southern Great Barrier Reef, respectively; SL, sea level; SOI, southern oscillation index; *LatDist*, latitudinal distribution; *PLD*, pelagic larval duration; *MaxLength*, maximum total body length; *CoralDep*, coral habitat dependence; *Troph*, trophic level.

Intercept-only model also included. For each model, we specify the covariates, random variables and traits included. We also indicate whether phylogeny was considered. We provide the number of sampling units and species, as these varied depending on data availability. AUC is the area under the receiver-operating characteristic curve. A full list of model rankings is provided in Table S2

FIGURE 4 Relative importance of the predictor variables included in the top-ranked joint species distribution model (see Table 1). The fixed variables are sea level (SL), southern oscillation index (SOI), local sea-surface temperature (SST) and SST at the southern Great Barrier Reef (SST$_{GBR}$). The random variables are location and year. The density plots represent the values estimated for all species in the dataset. The horizontal point-range lines show the mean ± 1 *SD* of each predictor variable [Colour figure can be viewed at wileyonlinelibrary.com]
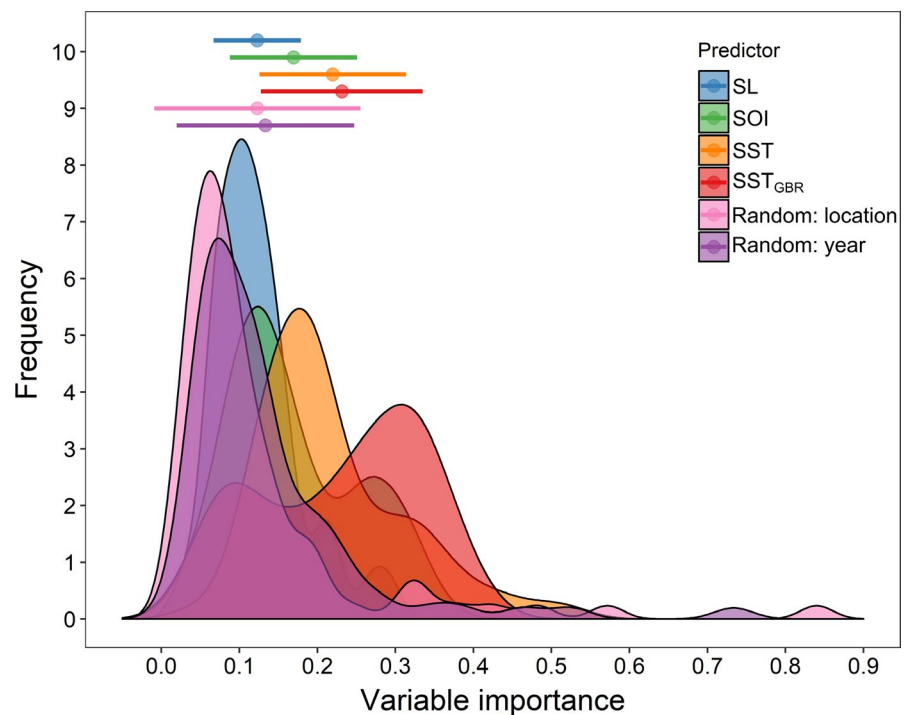
last sampling units differ, model support probability $p = 0.98$) and coral habitat dependence ($p = 0.99$), higher sea level linked to larger maximum total body length ($p = 0.97$), higher southern oscillation index favoured species with longer pelagic larval duration ($p = 0.99$), while trophic level was not related to any of the covariates. The random effects given by location and year accounted for only 12.3% and 13.3% of the variance respectively (Figure 4, S2).

Because the importance of some variables appeared to exhibit more than one mode (Figure 4), we performed tests of bimodality based a method proposed by Ameijeiras-Alonso et al. (2019), which combines the critical band-width and excess mass statistics to tests the null hypothesis of unimodality based on a nonparametric bootstrap procedure. The tests suggested a bimodal frequency distribution only for sea-surface temperature experienced by the

potential source populations at the southern Great Barrier Reef, centring at 0.1 and 0.3 (Figure 4; excess mass = 0.093, $p = 0.062$). This was explained by differences in the species composition between locations. While the hump centred at 0.1 was attributed to species that were recorded at both the *mixing* and *temperate* locations (25.0% of species recorded only at the *mixing* location, 0% only at the *temperate* location and 75.0% at both locations), the hump centred at 0.3 was produced mostly by species that only occurred at the *mixing* location (68.2% of species recorded only at the *mixing* location, 13.6% only at the *temperate* location and 18.2% at both locations). We found little support for bimodality in the frequency distribution of the other covariates (SL: excess mass = 0.059, $p = 0.506$; SST: excess mass = 0.072, $p = 0.148$; SOI: excess mass = 0.067, $p = 0.353$).

The joint species distribution model also indicated that the observed species richness was more strongly related to sea-surface temperature (both source and mixing/temperate fish survey locations) than to sea level or the southern oscillation index (Figure 5). Separating the species richness data by location, we revealed groupings (Figure 5) that suggest differential effects of the covariates on the assemblage dynamics of our *mixing* and *temperate* locations. Similar values of environmental covariates between locations were associated with generally higher species richness at the *mixing* location than the *temperate* location (Figure 5).

3.4 | Inferred species associations

The random component of the highest-ranked joint species distribution model captured residual associations among species (Fig. S4).

The residuals linked to year-to-year variability, which we used here to infer species-to-species associations, indicated that the number of non-random interspecific tropical species associations (with at least 95% posterior probability support) were low (n = 50) relative to the maximum possible (n = 3,240). We expected few associations given the low relative importance of the random variables detected by the models (13.3% of total variance for year; Figure 4). All supported associations were positive. Every species involved in such associations, except one (*Ctenochaetus binotatus*, ctbi), characteristically form schools (Fig. S4).

We used the species-association matrix and our occurrence time series to derive dynamics in the intensity of associations over the period of the study. We scored the positive and nil species associations detected by the model as ones and zeroes, respectively, and described the temporal dynamics using logistic regressions. Given the few
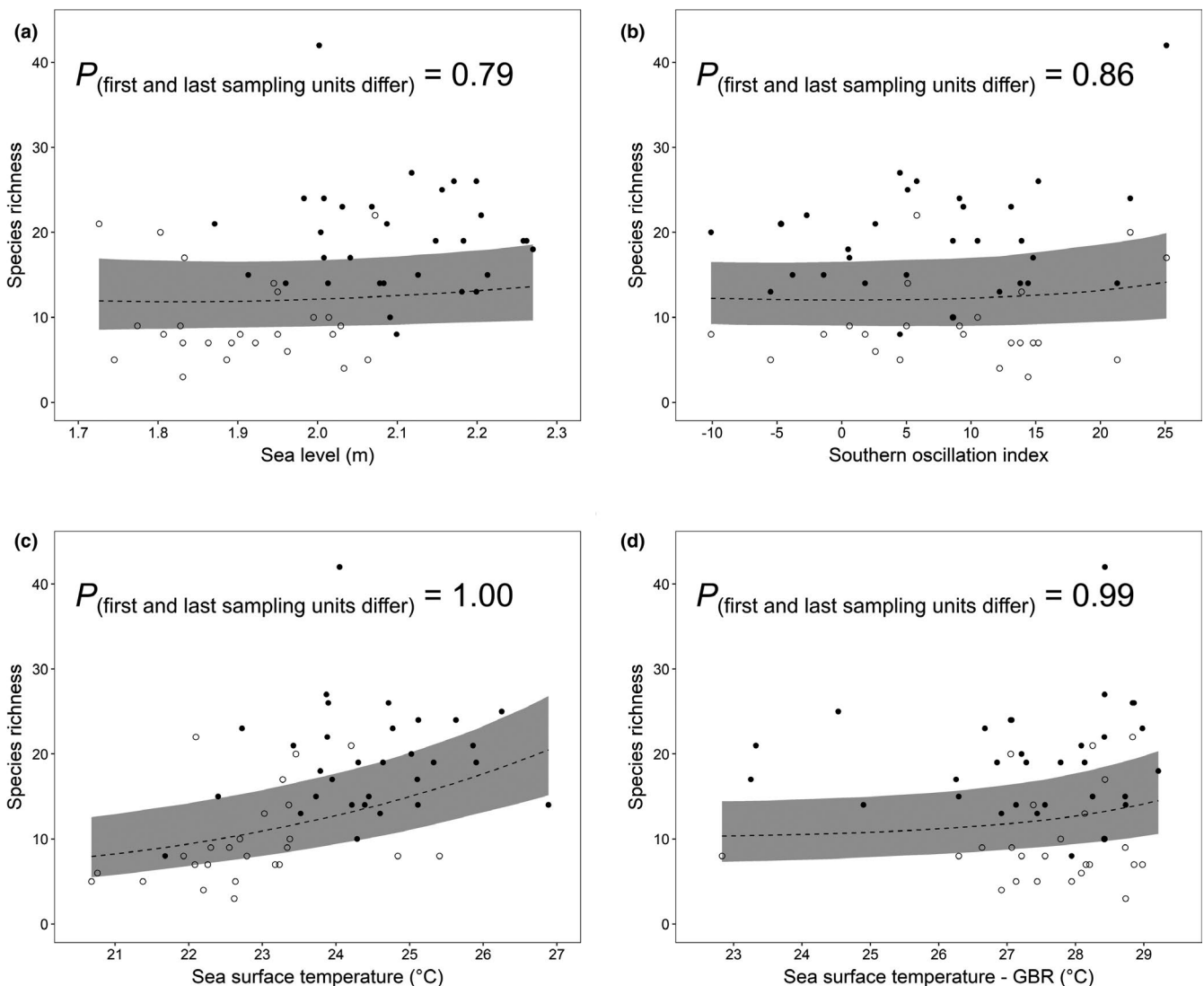

FIGURE 5 Species richness in relation to the covariate environmental factors included in the top-ranked joint species distribution model: (a) sea level, (b) southern oscillation index, (c) local sea-surface temperature and (d) sea-surface temperature at the southern Great Barrier Reef. Points represent observations at the *mixing* (black points) and *temperate* (white points) locations. Joint species distribution model predictions are illustrated by the dashed lines (posterior mean) and shaded areas (95% credible interval). The posterior probabilities that the last sampling unit differs from the first one are also provided

possible associations detected for these species, we found that the intensity of associations has remained close to zero, albeit increasing slightly over time at both the *mixing* and *temperate* locations (Fig. S5).

4 | DISCUSSION

Our quantitative analyses confirm that natural climatic oscillations can boost the range expansions of assemblages that are already responding to human-driven climate change. While previous studies have highlighted the importance of considering both natural and anthropogenic drivers to understand species range dynamics forced by climate change (e.g. Bates et al., 2014; Hilbish et al., 2010; Wethey et al., 2011), few have modelled these effects using long-term, assemblage-level empirical datasets. Using trends derived from classic diversity indices (richness, species accumulation, β-diversity [and its components]), we characterized changes in the assemblage composition of tropical fishes arriving at a *mixing* and a truly *temperate* location, generally confirming previous reports of increasing presences of tropical fishes in this region (Bates et al., 2014; Booth et al., 2007; Fowler et al., 2017). While the *temperate* location appears to be receiving tropical fish species at a higher rate (based on the time versus species-richness relationships), the *mixing* location consistently harbours a higher richness of vagrant species.

Perhaps more importantly, we detected an anomaly in the structure of this tropical assemblage during the strong La Niña period of 2010–2011 at both locations. While this signal was evident from the species-richness index alone, decomposing the β-diversity into its components provided a more nuanced perspective. During non-La Niña periods, the processes of species replacement and richness differences alternated in importance, with little variation in similarity values. These cycles indicate that, relative to the baseline year 2003, tropical assemblages pivoted between periods of species gains and losses (i.e. richness differences) and periods of species replacements (Legendre, 2014). During the 2010–2011 La Niña event, the increase in richness and decrease in replacement were especially strong (particularly at the *mixing* location), and this was accompanied by a decrease in similarity relative to the reference year. Although the differences between locations depend on the relative composition of their reference assemblages, which differed, the reduction in assemblage similarity forced by an influx of several *new species* and low replacement values registered were defining features of the La Niña event in this temperate region.

Previous studies have also reported a positive contribution of La Niña phases on the poleward expansion of marine organisms that disperse as plankton along the Australian coastline (e.g. Pearce & Hutchins, 2009; Wilson et al., 2018). Pearce and Hutchins (2009) found that the recruitment of tropical damselfishes on temperate shores of southwest Australia were greatest during La Niña 1999–2000. Similarly, Wilson et al. (2018) reported positive correlations between the southern oscillation index and the density of recruit and juvenile fish species, macroalgae and corals. Both studies

attributed the increased tropical vagrancy to the intensified southward Leeuwin Current and the associated warmer sea-surface temperatures. In contrast, a study along the Great Barrier Reef found that the abundances of damselfishes were generally favoured by conditions brought by the opposite ENSO phase of El Niño, although the effects varied along the reef (Cheal et al., 2007). While the study by Cheal et al. (2007) was done within the geographical range of the species and over a shorter time frame than ours, their results serve to highlight complex processes that contribute to the patterns of fish population dynamics along tropical reefs. Indeed, their results are explained by the observation that topographic complexity of the Great Barrier Reef can alter the hydrodynamics and the thermal conditions expected from natural climate oscillations (Dight et al., 1990; Redondo-Rodriguez et al., 2012). Differences in the physiological responses to environmental covariates between studies and regions could also explain discrepancies. For instance, if the thermal safety margin of the populations (i.e. the difference between an individual's local environmental temperature and its critical thermal maximum) differs between studies and regions, contradicting conclusions could arise. Differences in the landscape of ecological interactions could also play an important role in the dynamics of the species considered (Vergés et al., 2014). Ultimately, contrasting results between these or other biogeographical studies examining range shifts highlight the importance of accounting for the multiple physical and biological processes that can control the dynamics of populations and communities (Bates et al., 2014; Harley & Paine, 2009; Hilbish et al., 2010; Wethey et al., 2011). The joint species distribution models we used provided the means to assess quantitatively the roles of biotic and abiotic sources of variability on the long-term range shifts of these tropical vagrant fish assemblages.

Of the predictors we assessed, sea-surface temperature was indeed the most important in explaining fish-assemblage composition, with positive responses for many of the species we examined. The model indicated that the variance explained by the sea-surface temperature presumably experienced by the potential parents of the surveyed fishes at the Great Barrier Reef was comparable, although marginally higher, than the local sea-surface temperature. However, this result was influenced by the differences in species composition between the *mixing* and *temperate* locations, which forced a bimodal distribution in the importance attributed to the source-population sea-surface temperature, suggesting a greater importance of this covariate at the *mixing* than the *temperate* location. Nevertheless, these results indicate that species vagrancy and range shifts can generally benefit from warmer conditions both at the source and sink populations. Higher temperatures experienced by the source population within the species' thermal tolerance window could increase the fertility of parents (Pankhurst & Munday, 2011; Pörtner & Farrell, 2008). After settling in temperate locations, higher temperatures could either enhance the physiological performance of these tropical fishes (McCormick et al., 1995), or reduce thermally sensitive predation rates (Fig ueira et al., 2019).

According to our models, changes in sea level (a proxy for the strength of the East Australian Current) had little influence on the

dynamics of this tropical vagrant assemblage. This was unexpected based on previous studies supporting a link between an intensified southward transport (Ridgway, 2007) and higher numbers of tropical species in the temperate zone (Booth et al., 2007; Fowler et al., 2017; Ling et al., 2009), but further inspection of the temporal trends in sea level revealed that the potential advection of larvae had increased only at the *mixing* location (Fig. S6). This explains the weak effect of this covariate on assemblage composition. Because the poleward flow of the East Australian Current diverges offshore at ~ 32 °S latitude, giving rise to coastal eddies with turbulent trajectories (Suthers et al., 2011), the advective larval transport towards our *temperate* location is reduced (Fowler et al., 2017), resulting in generally lower richness and β-diversity. The different pool of species arriving at each location helps explain a bimodal distribution in the importance of the sea-surface temperature experienced by parents at the potential source population, because most species with a higher dependence for this covariate settled only at the *mixing* location.

The joint species distribution model also estimated the influence of the background signal of the ENSO on assemblage dynamics, and captured the 2010–2011 anomaly in species composition. The southern oscillation index was less influential than sea-surface temperature because it affected assemblage dynamics over shorter periods. Nevertheless, despite its acute mode of action, the strong La Niña event led to the highest species richness and diversity that we recorded, thus explaining its relatively high contribution to assemblage dynamics. While the overall influence of ENSO on species composition was similar at our two locations, the instantaneous effect of the La Niña event was relatively stronger at the mixing location. This result, along with the uneven contribution of the East Australian Current to the supply of larvae to these locations, stresses the importance of considering spatial-temporal nuances that mediate the effects of anthropogenic climate change and natural climate oscillations on the range shifts of coastal species (Harley & Paine, 2009).

A distinction between anthropogenic climate change and natural climatic oscillations is that the former tends to be more gradual and protracted (i.e. chronic effects), whereas the latter often manifests as abrupt change (i.e. acute effects) (Krokos et al., 2019). The structure of the emergent assemblage is a consequence of their cumulative effects, which can be additive, antagonistic or synergistic (Hilbish et al., 2010; Wethey et al., 2011). Our analyses suggest additive effects for the period examined, because the strong positive phase of the southern oscillation (i.e. La Niña) exacerbated the climate change-related poleward shift of tropical vagrant fishes. The long-lasting consequences of these cumulative impacts can be gauged by those species that entered our locations for the first time in 2010–2011, and reoccurred thereafter. Overall, the fact that several of these species did not reoccur at our locations stresses the independent role of ENSO on the dynamics of this range shift. Additionally, the different proportion of species reoccurrences between our locations further suggests that the process of tropicalization is following different trajectories across this temperate region. The fact that several of these species were absent from our

surveys during the 2014–2015 El Niño indicates that this tropical assemblage's range shift still depends on the aggregate effect of both the ENSO cycle and anthropogenic climate change. While the acute effects of the former can erode dispersal barriers and allow the arrival of new species, their subsequent establishment in the region is possible only if the long-term climate can meet the physiological requirements of these tropical vagrants (Bates et al., 2014; Booth et al., 2018). While it is difficult to predict confidently which tropical species will occupy this now-temperate region in the future, the finding that some quantifiable traits were positively associated with the environmental covariates—notably species with wide latitudinal distribution and strong coral-habitat dependence favoured by warming, or those with long pelagic larval duration linked to the ENSO signal—provides a means to anticipate which functional traits might dominate in novel communities.

We found little evidence for species associations in this tropical assemblage, but when detected, these were all positive. In contrast to a previous study (Booth et al., 2007), our model did not detect an association between the butterflyfishes *Chaetodon auriga* and *C. flavirostris*. However, the discrepancy could be due to differences in methodology. While that previous study used correlation tests to examine co-occurrences in isolation, our models quantify associations after accounting for environmental covariates (Ovaskainen et al., 2017). Despite the robustness of this method and given the low prevalence of many of the species in our study, we could have missed some associations; nevertheless, our analysis produced a useful perspective on the generalized association network of this range-shifting assemblage. Positive associations increased during the course of the study, particularly after the strong La Niña. Previous investigations on the range dynamics of multiple species have emphasized the importance of main consumers or habitat-forming taxa (Kumagai et al., 2018; Martínez et al., 2018; Yamano et al., 2011). As most of the associations we inferred took place between schooling species, our model supports the notion that grouping dynamics might also contribute to the initial establishment of these species (Paijmans et al., 2019).

The ongoing warming of the sea and increased larval transport due to anthropogenic climate change are gradually expanding the poleward edge of tropical species distributions in both hemispheres (e.g. Fowler et al., 2017; McLean et al., 2018; Monaco, Nagelkerken, et al., 2020). We show that natural climatic variation can exert a strong additive effect, which can rapidly modify the pool of incoming species threatening to disrupt local communities. These effects will likely compound with the ecological impacts of extreme weather events (e.g. storms, heat waves), which are increasing in frequency and intensity as a result of climate change (Oliver et al., 2019). Therefore, anticipating ecological changes in the receiving community call for an understanding of the complex feedbacks between climate change, via both mean and extreme effects, and natural climatic oscillations (Meehl et al., 2006; Yeh et al., 2009).

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BIOSKETCH

Cristián J. Monaco is a marine biologist interested in eco-physiological processes that can improve our understanding of the mechanisms driving natural systems' responses to environmental variables. He favours an integrative approach combining field and laboratory observations and manipulations, along with computer modelling.

Authors contributions: All authors contributed to the original concept. C.J.M. chose the analyses. C.J.M. did the analyses and led the writing. All authors contributed to the writing of the manuscript.

SUPPORTING INFORMATION

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

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