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RESEARCH ARTICLE

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Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems

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Abstract

1. Climate change is modifying species distributions around the world, forcing some species poleward, where they can alter trophic interactions. Many tropical herbivorous fishes have successfully expanded their ranges into temperate ecosystems, and while it is clear they drive increases in herbivory rates in specific localities, little is known about how they might affect the diversity of herbivory functions across large spatial scales, considering their interaction with assemblages of native herbivores in temperate habitats.
2. We assessed the spatial overlap and habitat associations of native temperate and range-expanding tropical herbivorous fishes in six subregions of south-western Australia to determine how incursions of tropical species may have affected the diversity, redundancy (index of uniqueness) and the 'spatial extent' (addition of functions in new areas) and 'intensity' (increasing density of functional groups) of specific herbivory functions in recipient ecosystems.
3. Tropical herbivores had high abundances in temperate ecosystems, forming schools from 40 (parrotfish) to 200 (rabbitfish) individuals strongly associated with seagrass meadows and reefs with high cover of turf algae. Overlap with temperate herbivores was highest in the northern subregions, forming unique assemblages, with no apparent species displacements. The addition of tropical species increased functional diversity and uniqueness (the complement of redundancy), introducing novel herbivory functions to many locations. Seagrass browsing increased in spatial extent (27%) and intensity (15×), while seaweed browsing and grazing increased in intensity by up to 2.5× in regions with high abundances of tropical herbivores.
4. Our results suggest that the diversity, intensity and spatial extent of different herbivory functions can change as tropical species with different habitat affinities, behaviours and diets shift their distributions poleward. Changes in functional redundancy are likely to be heterogeneous in space and might not increase initially because the diversity of herbivory functions is relatively low in some temperate marine ecosystems. However, there is the potential for greater redundancy

as further tropical species arrive, their abundances increase and the spatial and functional overlap of communities rises.

KEYWORDS
climate change, habitat associations, herbivory, novel interactions, range-shifts, spatial overlap, tropicalization

1 | INTRODUCTION

Evidence is mounting about the impact of climate change on the distribution of marine and terrestrial species (Pecl et al., 2017). While species' ranges are expanding, contracting or shifting locally, overall there is a global trend for species' addition at higher latitudes (Blowes et al., 2019). This trend has seen an increase in the proportion of species of tropical affinity in temperate ecosystems, a process often referred to as 'tropicalization' (García Molinos et al., 2015; Wernberg et al., 2012). Tropicalization has been particularly strong in marine ecosystems (Vergés et al., 2014), where climate-change velocities and species range-shifts are advancing at higher rates than in terrestrial environments (Burrows et al., 2011; Sorte, Williams, & Carlton, 2010). Range expansion of tropical species into temperate regions alters the species composition of recipient ecosystems, potentially changing the diversity and intensity of ecological functions, in ways that depend on the outcomes of novel species interactions and the overall balance between species extirpations and additions in the ecosystem (Albouy et al., 2014; Ockendon et al., 2014).

As novel species assemblages emerge, ecological processes can be modified by ecological engineers (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013). Temperate seagrass meadows and kelp forests are forecast to change as the ocean warms, because top-down forces are expected to intensify with the addition of tropical herbivores (Hoekman, 2010; Hyndes et al., 2016). Herbivory is a key ecological function which regulates the bottom-up energy flow between trophic levels and the top-down control on habitat structure by reducing seagrass and seaweed canopy cover and mediating competition for space between sessile taxa (Nowicki, Fourqurean, & Heithaus, 2018; Poore et al., 2012). Consequently, the strengthening of herbivory by range-extending tropical herbivores could shift temperate habitats primarily regulated by production towards states regulated by consumption (Vergés et al., 2014), thereby accelerating the integration of biomass from habitat-forming macrophytes into the food chain (Zarco-Perello, Langlois, Holmes, Vanderklift, & Wernberg, 2019) and increasing the cover of turf seaweed and sessile invertebrates (Filbee-Dexter & Wernberg, 2018; Ling, Barrett, & Edgar, 2018).

The effect of range-expanding tropical herbivores will likely depend on the magnitude of functional overlap with existing temperate herbivore assemblages. Novel species associations can result in competition, causing replacements of species and ecological functions (Milazzo, Mirto, Domenici, & Gristina, 2013), or creating new assemblages that augment certain ecological processes (Marshak & Heck, 2017). Herbivorous fishes, particularly species from the family Siganidae, have been some of the most successful at expanding their distributions poleward (Vergés et al., 2014). Current evidence suggests that where they have expanded, there has not been a displacement of temperate species but rather additions of new populations (Bennett, Wernberg, Harvey, Santana-Garcon, & Saunders, 2015; Vergés et al., 2014; Zarco-Perello et al., 2019; Zarco-Perello, Wernberg, Langlois, & Vanderklift, 2017).

Herbivory is carried out by species with different feeding behaviours that are generally classified into two broad functional groups: 'grazers', which bite on reef substrata and regulate recruitment rates of sessile taxa by consuming turf seaweed, sediment and particulate organic matter; and 'browsers', which bite at canopy-forming macrophytes, engineering the three-dimensional habitat structure of the ecosystem (Bellwood, Streit, Brandl, & Tebbett, 2019). Consequently, increases in the number of herbivorous species could intensify herbivory by adding to the number and richness of functional groups present. However, considering that species have specific habitat associations, diet preferences, consumption rates and population sizes (Ruttenberg, Adam, Duran, & Burkepile, 2019), high spatial variation in functional changes and in the degrees of ecological impacts on primary producers can be expected as novel guilds of herbivores are formed.

Knowledge of the habitat associations of range-shifting species is needed in order to evaluate their interactions, identify which habitats are more likely to be affected and which ones are likely to facilitate further range expansions of tropical species. However, this has rarely been considered in range-shift predictions (Parravicini, Azzurro, Kulbicki, & Belmaker, 2015) and currently we lack an understanding of how range-shifting tropical species can affect herbivory functions in different habitats across large spatial scales (Bonebrake et al., 2018). The spatial overlap of temperate and range-expanding tropical herbivores will determine changes in functional diversity and redundancy of herbivory; however, since many species have functional plasticity (i.e. they can graze or browse on different macrophytes; Bennett et al., 2015; Ebrahim, Martin, Mumby, Olds, & Tibbetts, 2020; Zarco-Perello et al., 2019), the execution of each function also depends on the spatial overlap between consumers and food resources. The concept of spatial overlap within ecological communities has been applied to estimate trophic interactions between species of predators and their prey (e.g. Carroll et al., 2019), but has not been applied to functional analyses of herbivory. Here we use this approach to assess novel species interactions between potential competitors (tropical and temperate herbivores) and their associated effects on herbivory in temperate marine habitats experiencing tropicalization (Wernberg et al., 2016). For this, we evaluated (a) the habitat associations and spatial overlap of temperate and range-expanding tropical herbivores, (b) the relative effect of tropical herbivores on functional diversity and (c) changes in the spatial extent (addition of functions in new areas), and intensity (increasing density of functional groups) of specific herbivory functions.

2 | MATERIALS AND METHODS

2.1 | Study location

The composition of fish assemblages in coastal habitats of western Australia has changed following a marine heatwave that struck the region in 2011 (Wernberg et al., 2016). Tropical rabbitfish *Siganus fuscescens* have since formed self-recruiting populations in temperate ecosystems (Lenanton, Dowling, Smith, Fairclough, & Jackson, 2017; Zarco-Perello et al., 2019) while parrotfish *Scarus ghobban* and *S. schlegeli* became more abundant (Parker et al., 2019). To identify the effects of these changes, surveys of herbivorous fish were conducted over inshore habitats along the coastline of southwestern Australia during summer (April–May) of 2018 and 2019, from the Perth metropolitan area to Cape Naturaliste in the south of the state. The ecosystems along the coast consist of carbonate reefs interspersed with boulder reefs, seagrass meadows and sandy plains. Survey locations were restricted to shallow habitats (depth 1–9 m; up to 6 km from the shoreline), where the abundance of herbivorous fish is highest (Hoey, Brandl, & Bellwood, 2013).

2.2 | Herbivorous fish abundance and habitat associations

The abundances of temperate (*Girella zebra*, *Olisthops cyanomelas*, *Pelates octolineatus*, *Kyphosus cornelii* and *Kyphosus sydneyanus*) and tropical herbivorous fish (*Scarus* spp. and *Siganus fuscescens*) were measured via a GPS-tracked roving underwater visual census with 15 min per sampling location. This method is effective to estimate the abundance of schooling herbivorous fish and has proven to be efficient for range-shifting species (Beck, Feary, Figueira, & Booth, 2014; Fox & Bellwood, 2008). One roving survey was performed per site, where one surveyor swam at a constant pace, registering all individuals of the species of interest in an approximate area of 2,000 m^2. A second surveyor followed the same path recording the seascape with an underwater camera for subsequent assessment of habitat features. Videos were analysed with the program TransectMeasure (SeaGIS), each video transect was paused at 1-min intervals ($n = 15$ per transect) to extract information on topographic complexity (Wilson, Graham, & Polunin, 2007), substrate type, species composition, species diversity and abundance of morphofunctional groups of sessile biota based on the CATAMI classification scheme (Althaus et al., 2015). A total of 69 sites were surveyed across six subregions: North Perth (31.8°S, $n = 13$), Rottnest Island (32°S, $n = 18$), South Perth (32.2°S, $n = 13$), Rockingham (32.4°S, $n = 11$), Bunbury (33.3°S, $n = 5$) and Geographe Bay (33.6°S, $n = 9$). The relationship between the herbivorous fish assemblage and selected measurements of habitat was assessed using a canonical correspondence analysis (CCA; Borcard, Gillet, & Legendre, 2011) with the R package VEGAN (Oksanen et al., 2019).

Fish abundance was standardized to density (individuals 125 m^{-2}); however, we also considered a new metric: MaxS (maximum number of fish per school in each survey), a similar approach to abundance assessments of pelagic schooling fish (i.e. school size; Beare, 2002) and abundance estimates from static video methods (i.e. MaxN; Cappo, Harvey, Malcolm, & Speare, 2003). In addition to abundance information, MaxS can be a proxy for reproductive behaviour (Azzurro, Franzitta, Milazzo, Bariche, & Fanelli, 2017) and ecological impact, since certain species have positive correlations between school size and per capita consumption rates (Basford et al., 2016; Michael, Hyndes, Vanderklift, & Vergés, 2013). For simplicity, we report the highest MaxS and the average MaxS (MaxSm) per subregion in the text. Changes in abundance of temperate and tropical herbivorous fish across latitude were evaluated in separate models with negative binomial generalized linear models using the R package GLMMTMB (Brooks et al., 2017).

2.3 | Herbivorous fish spatial overlap

The potential strength of ecological interactions between tropical and temperate herbivorous fish species was estimated by calculating their spatial overlap with the 'local index of colocation' (Pianka's *O*; Carroll et al., 2019; Pianka, 1973). This metric assesses the correlation between the proportions of the densities of two groups across sites, and can be considered a proxy for their encounter rate (Carroll et al., 2019; Pianka, 1973). For this analysis we pooled the densities of all tropical herbivorous species and all temperate herbivorous species and calculated the overlap between the two groups within each subregion. A resampling jackknife method was applied to estimate mean and standard errors of overlap within each subregion, where we repeatedly recalculated Pianka's *O*, each time excluding a different site from the calculations (Manly, Chatfield, Tanner, Carlin, & Zidek, 2007).

2.4 | Diversity and spatial overlap of herbivory functions

We classified herbivory functions based on the tendency of species to feed on different groups of macrophytes that affect different ecological processes: (a) grazing of turf (impacting sessile taxa recruitment), (b) browsing on seaweed canopy (impacting habitat structure) and (c) browsing of seagrass canopy (impacting nursery grounds). Because each herbivorous species contributes differently to each function (Hoey & Bellwood, 2009), we assigned them a species-specific weight based on herbivory rates and stomach content analyses reported in the scientific literature, as well as observations during our surveys in the region (Table S1). Changes in overall herbivory functions in each temperate subregion were assessed by calculating functional diversity (FD) based on attribute diversity ($t = d_{\text{mean}}$ and $q = 1$, Chao et al., 2019) and functional uniqueness (U, the complement of redundancy), employing the function *uniqueness* with Euclidean distance (Table S2) using the software R (R Core Team, 2019): $U = Q/D$, where U is uniqueness, Q is Rao quadratic entropy (an index of functional diversity) and D is the Simpson index of biological diversity (Ricotta et al., 2016). The creators of the U index exemplify its application to analyse the vulnerability of ecosystems to population declines or species extinction due to disturbances, here we apply it to analyse the impact of species additions due to range shifts.

To assess changes in specific herbivory functions, we performed spatial overlap analyses to calculate addition of functions in new areas (i.e. increase in spatial extent) and increase in intensity of existing functions across space (i.e. increase in density). Functional weights were not scaled for these calculations and only adult individuals were included in these analyses, since herbivory rates of juveniles of most species are uncertain.

Herbivory intensity was calculated with a modified version of community weighted mean of trait values (Laliberté & Legendre, 2010) that incorporates spatial overlap. We refer to this as the overlapped community weighted mean of trait values (oCWM), where we accounted for the execution of specific herbivory functions only when there was overlap between each functional group of herbivores (e.g. seagrass browsers) and the group of macrophytes they consume (e.g. seagrass), similar to analyses of predator–prey interactions (Figure 1a; Carroll et al., 2019; Pianka, 1973). For each herbivory function, we defined the spatial range of its corresponding macrophyte type (seagrass, turf and canopy seaweed) based on whether it occurred at each survey site across the region. Within the range where the macrophyte was present, the densities of each temperate and tropical herbivorous species were multiplied by their weight value for that function. For instance, species with a weight value of 0 for seagrass browsing did not contribute to that function despite them being very abundant, whereas species with values >0 contributed only where the populations overlapped with seagrass meadows. The effect of tropical herbivores for each herbivory function in each subregion was then determined as the increase in oCWM including tropical species (mixed ensemble), relative to the oCWM of temperate species alone (Figure 1). Statistical significance of observed variations between temperate and mixed ensembles in all functional indices within each subregion were tested with permutational multivariate analysis of variance (PERMANOVA) using the function *adonis* of the R package VEGAN (Oksanen et al., 2019). Herbivory extent was calculated as the 'range overlap' between each macrophyte and its consumers (Carroll et al., 2019). For this, we took the spatial range for each macrophyte and then determined their overlap with their corresponding herbivory function considering the presence of only (a) temperate consumers, (b) tropical consumers and (c) either temperate or tropical consumers. The difference between temperate consumer overlap and the overlap between either temperate or tropical consumers represented the increase in herbivory extent attributable to the addition of tropical herbivores (Figure 1).

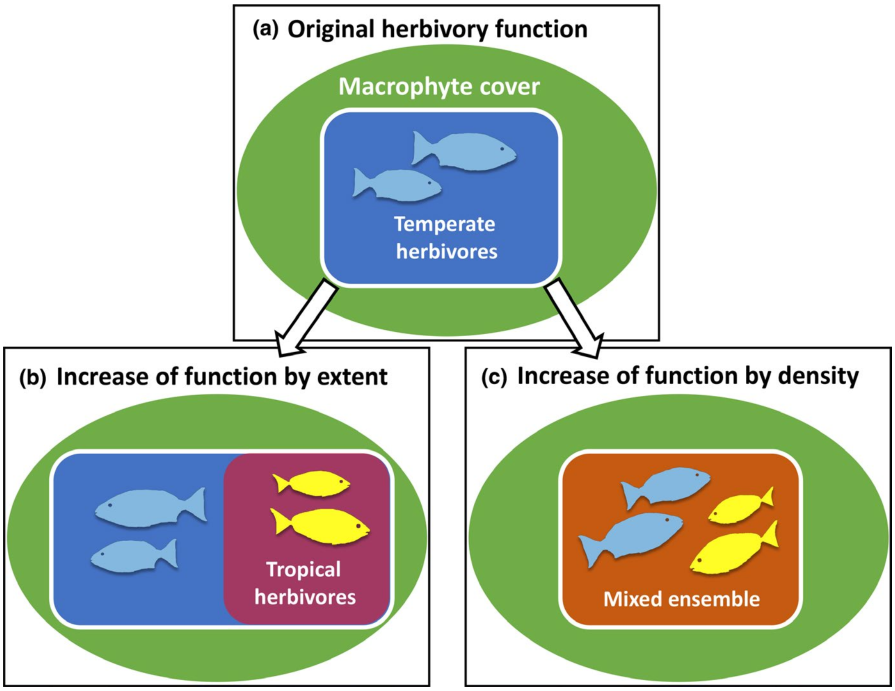

FIGURE 1 Conceptual diagram of the overlap analyses used to assess changes in herbivory functions in temperate ecosystems due to the overlap of tropical and temperate herbivores and the macrophytes they consume (a). Changes in *spatial extent*: changes in area overlap between herbivory functions and corresponding macrophytes by the arrival of tropical species (b), and *intensity* (*density*): calculated as overlapped weighted mean of traits of functional groups of temperate and tropical herbivores (mixed ensemble) within spatial ranges of corresponding macrophytes (c)

3 | RESULTS

3.1 | Spatial overlap of temperate and tropical herbivores

Abundance of tropical herbivores declined as latitude increased (GLM, $p < 0.01$), as did the abundance of temperate herbivores (GLM, $p = 0.035$). Temperate herbivores were more abundant than tropical herbivores in all subregions (Figure 2a). Tropical rabbitfish were frequently seen at North Perth (MaxSm: 60 ± 19 (mean individuals school^{-1}), MaxS: 207 (maximum school size)) and around Rottnest Island (MaxSm: 24 ± 9.5; MaxS: 158). In South Perth, rabbitfish were recorded less frequently (MaxSm: 10 ± 8; MaxS: 100) but here we registered the only school of juveniles (MaxS: 100). No rabbitfish were recorded at Rockingham or Bunbury, but they were observed at Geographe Bay (MaxSm: 10.4 ± 7.9; MaxS: 100). Parrotfish populations were only recorded at Rottnest Island, where they were generally abundant (MaxSm: 6 ± 2.3; MaxS: 39). Temperate herbivores were recorded at all study sites but with varying abundances. *Kyphosus sydneyanus* was observed across the entire latitudinal gradient and was most abundant at North Perth (MaxSm: 35.4 ± 8; MaxS: 96), Rottnest Island (MaxSm: 45.1 ± 23.5; MaxS: 404) and Rockingham (MaxSm: 38.5 ± 13.9; MaxS: 141). *Kyphosus cornelii* had similar patterns, having high abundances at North Perth (MaxSm: 39.5 ± 11.5; MaxS: 130), Rottnest Island (MaxSm: 99.5 ± 15.0; MaxS: 290) and Rockingham (MaxSm: 38 ± 18; MaxS: 162). *Pelates octolineatus* was most abundant at South Perth (MaxSm: 48.4 ± 27.5; MaxS: 360), Rockingham (MaxS mean: 102.9 ± 46.5; MaxS: 465), and Geographe Bay (MaxSm: 24.1 ± 10.2; MaxS: 95). *Girella zebra* was abundant at Rottnest Island (MaxSm: 15.3 ± 9.3; MaxS: 153) and Geographe Bay (MaxSm: 2.2 ± 1.1; MaxS: 10). *Olisthops cyanomelas* was recorded in all the regions; however, as the only non-schooling herbivorous species in the study it generally had the lowest abundances, except for Geographe Bay (Figure 2b). Spatial overlap between temperate and tropical herbivores was highest in the most northerly subregions (Pianka's *O* at North Perth = 0.46 ± 0.01, Rottnest Island = 0.38 ± 0.01 and South Perth = 0.73 ± 0.06), with overlap decreasing towards the south (Pianka's *O* at Rockingham = 0, Bunbury = 0, Geographe Bay = 0.28 ± 0.01; Figure 2c).

3.2 | Habitat associations

Canonical correspondence analysis of the herbivorous fish community and habitat variables accounted for 82% of the total constrained inertia in the first two axes. The first axis represented a gradient from high latitude habitats dominated by canopy-forming and coarse-branching seaweed species (e.g. *Ecklonia radiata* and *Sargassum* spp.) to lower latitude sites with higher cover of turf (small-mixed seaweed); while the second axis represented a gradient of topographic complexity, from seagrass meadows to consolidated reef substrates covered by seaweeds (Figure 3). Along these gradients, the species scores aggregated in three main groups of herbivores; (a) *P. octolineatus* and *O. cyanomelas* were more strongly associated with habitats having higher cover of large brown seaweed at higher latitudes. However, *P. octolineatus* associated more with seagrass, whereas *O. cyanomelas* associated more with reefs. (b) *K. cornelii* and *K. sydneyanus* were associated more with reef sites with medium canopy-cover, while (c) *G. zebra*, *Scarus spp.* and the rabbitfish *S. fuscescens* were associated more with sites with seagrass meadows and reefs with higher cover of turf seaweed.

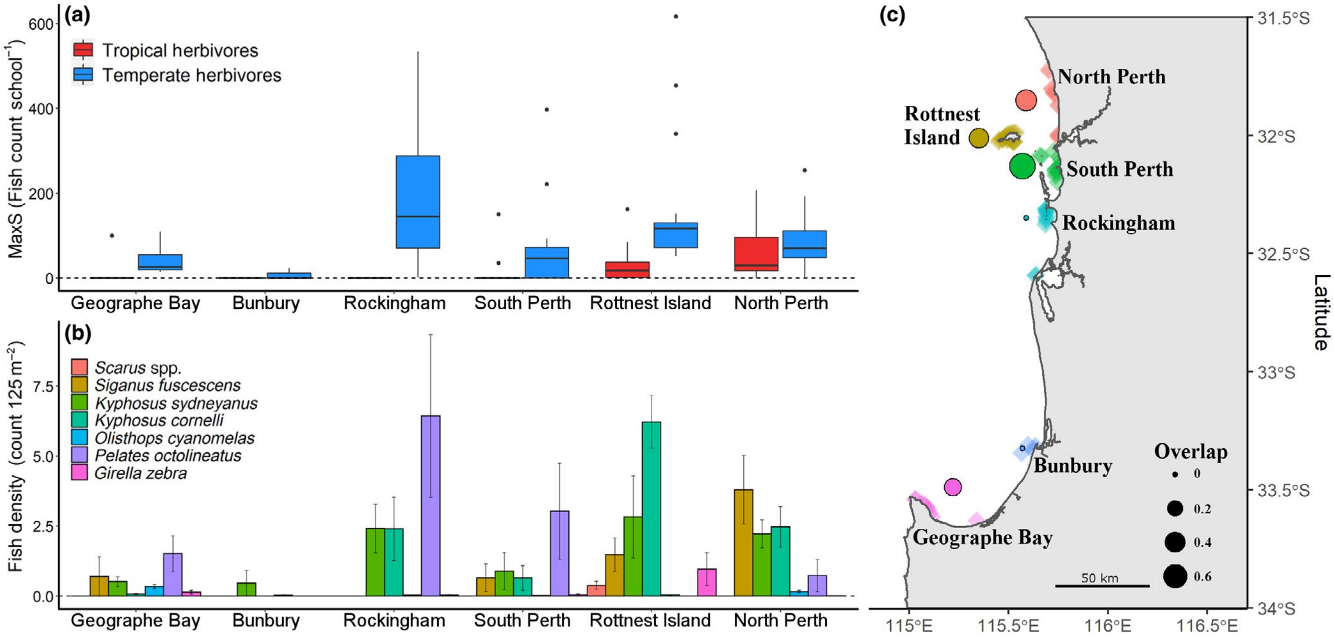

FIGURE 2 Abundance patterns as MaxS (school size) (a) and density (b) of herbivorous fish of tropical (*Scarus* spp. and *S. fuscescens*) and temperate climate affinity (*Kyphosus* spp., *O. cyanomelas*, *P. octolineatus* and *G. zebra*) and (c) their spatial overlap (Pianka's *O*) along the temperate subregions of Western Australia. Coloured diamonds in map represent surveyed sites

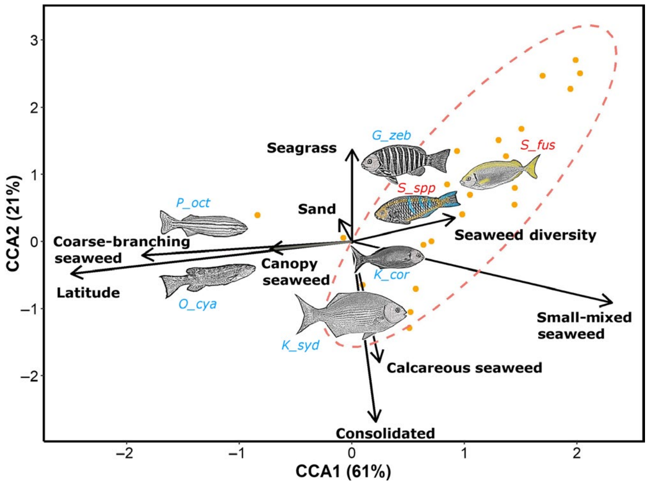

FIGURE 3 Canonical correspondence analysis of herbivorous fish species and habitat variables (arrows) of temperate ecosystems in southwestern Australia. Ellipse encloses sites (dots) where rabbitfish (*S_fus*) were recorded. *P_oct* = *Pelates octolineatus*; *O_cya* = *Olisthops cyanomelas*; *K_syd* = *Kyphosus sydneyanus*; *K_cor* = *Kyphosus cornelii*; *G_Zeb* = *Girella zebra*; *S_spp* = *Scarus* spp. and *S_fus* = *Siganus fuscescens*

Nonetheless, schools of parrotfish and especially rabbitfish, were also found at sites with high canopy cover, over reefs associated with low seagrass density and habitats with low and high topographic complexity, co-occurring with all temperate species in several sites (Figure 3).

3.3 | Functional diversity

The addition of tropical species increased average functional diversity (FD) and functional uniqueness whenever they established abundant populations (Figure 4). Considering only temperate herbivores, we found that Geographe Bay (1.68 ± 0.09) and North Perth (1.73 ± 0.14), the subregions at the highest and lowest latitudes respectively, had the highest FD; however, the addition of tropical species shifted the highest values towards lower latitudes, with high increases in North Perth (33% higher; 2.3 ± 0.2; PERMANOVA $p = 0.037$) and Rottnest Island (25% higher; 1.75 ± 0.11; PERMANOVA $p = 0.017$) with smaller or no increases in other regions with fewer or no tropical herbivores (South Perth = 1.3%, Rockingham = 0%, Bunbury = 0%, Geographe Bay = 2.5%; Figure 4a). Average functional uniqueness values were very similar in four out of six subregions considering only temperate communities, but as with FD, the inclusion of tropical species shifted the highest values towards northern latitudes, with North Perth being the highest (109% higher; PERMANOVA $p < 0.001$), followed by Rottnest Island (47% higher; PERMANOVA $p < 0.02$; Figure 4b).

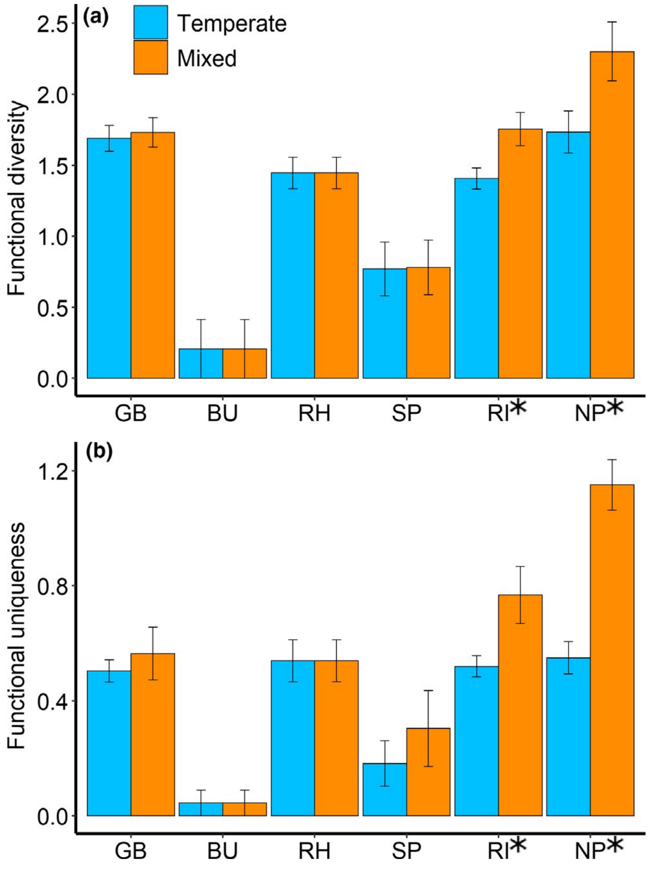

FIGURE 4 Variation ($M \pm SE$) of functional diversity (a) and functional uniqueness (b) considering communities of temperate herbivorous fish only, and with the addition of populations of tropical species (mixed) in south western Australia (GB: Geographe Bay, BU: Bunbury: RH: Rockingham, SP: South Perth, RI: Rottnest Island, NP: North Perth). Asterisks on bar charts mark statistically significant differences between temperate and mixed herbivorous communities (PERMANOVA $p < 0.05$)

3.3.1 | Herbivory functions

The addition of tropical herbivores contributed to a 27% increase in spatial extent of potential seagrass browsing. Of the 157.5 km^2 that was surveyed during this study, 106 km^2 represented sites where seagrass was present; of this area, 55% overlapped with temperate seagrass consumers, 47% overlapped with tropical seagrass consumers and 74% overlapped with either temperate or tropical seagrass consumers. Turf seaweeds were present across 147.5 km^2; of this area, 82% overlapped with temperate grazers, 45% with tropical grazers and 85% with either temperate or tropical grazers, thus representing an increase of 3% in spatial extent of potential seaweed grazing with the addition of tropical species. Canopy seaweeds were present across 129 km^2 of the survey area, 94% of this overlapped with temperate seaweed browsers, 48% with tropical seaweed browsers and 96% with either temperate or tropical seaweed browsers, representing an increase of 2% in spatial extent of potential seaweed browsing due to tropical herbivores.

Overlapped community weighted means of traits (oCWM) for all herbivory functions increased in the northern subregions (Figure 5; PERMANOVA $p < 0.02$). In the absence of tropical species, seagrass and seaweed browsing oCWM were highest at mid-latitude subregions, while seaweed grazing was highest at

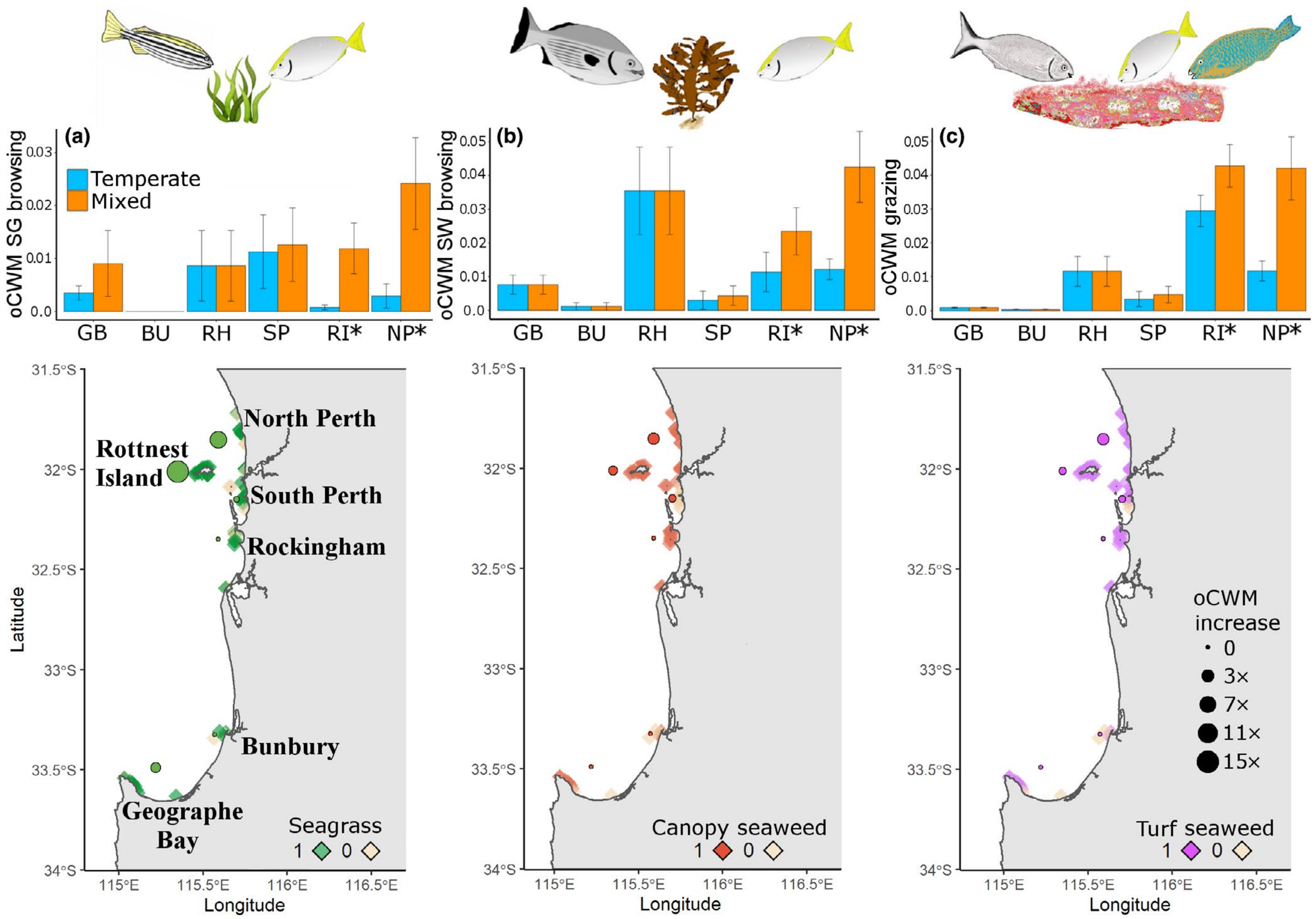

FIGURE 5 Variation in values (bars; $M \pm SE$) and relative increases (maps) of functional metrics considering communities of temperate herbivorous fish only, and with the addition of populations of tropical species (mixed). Overlapped Community Weighted Means of Traits for seagrass browsing (a), seaweed browsing (b) and seaweed grazing (c) across temperate western Australia (GB: Geographe Bay, BU: Bunbury: RH: Rockingham, SP: South Perth, RI: Rottnest Island, NP: North Perth). Asterisks on bar charts mark statistically significant differences between temperate and mixed herbivorous communities (PERMANOVA $p < 0.5$). The size of the bubbles in the maps represent proportional increase in herbivory functions with the addition of tropical species, coloured diamonds represent presence/absence of macrophytes at sampling sites

Rottnest Island. However, when tropical herbivores were mixed in the communities, Rottnest Island and North Perth had significant increases for average seagrass browsing (15× and 9× respectively; PERMANOVA $p = 0.02$), seaweed browsing (1× and 2.5× respectively; PERMANOVA $p = 0.02$) and seaweed grazing (0.4× and 2.6× respectively; PERMANOVA $p < 0.01$). Southern subregions had small or no changes in herbivory functions, except for Geographe Bay, which had an increase in seagrass browsing (1.6×), albeit not statistically significant (PERMANOVA $p = 0.97$).

4 | DISCUSSION

Our study assessed the spatial interactions between tropical and temperate herbivores and evaluated their effects on herbivory functions within temperate marine habitats along a latitudinal gradient. The range expansion and increase in abundance of tropical herbivores into higher latitudes did not appear to modify the abundance of temperate herbivores or cause species replacements. The northern subregions had the highest abundances and species diversity of temperate herbivores, but also had the highest abundances of tropical herbivores, as reflected in their high overlap values. This indicates that there is no negative relationship between temperate and tropical herbivores at the densities observed.

These results align well with the resource partitioning and empty niche theories proposed to explain the success of many invasive species (Lowry et al., 2012). This is particularly relevant for herbivorous species because temperate ecosystems generally have a surplus of macrophyte production and low competition (Mann, 2000). For instance, the Mediterranean Sea has extensive and productive seagrass and seaweed habitats (Sales & Ballesteros, 2012), yet hosts only two native herbivorous fish species (*Sarpa salpa* and *Sparisoma cretense*), which likely has eased the expansion of tropical herbivores in the region. *Scarus ghobban* remains uncommon in the Mediterranean Sea, but the occurrence of this species has extended from Israel to Greece (Erguden, Bayhan, Alagöz Erguden, & Altun, 2018), while the rabbitfish *Siganus luridus* and *Siganus rivulatus* have become abundant in many locations, attaining MaxS of ~100 individuals at the edge of their expansion in Linoza, Italy (Azzurro et al., 2017). The region of our study has a higher diversity, with five dominant species, but still lags far behind herbivore assemblages in the tropics with 30–100 species (Steneck, Bellwood, & Hay, 2017).

Our results on habitat associations also indicate that the different behaviours and diet of each species can facilitate coexistence of competitors. Some species were associated with reefs with different cover of canopy-forming and turf seaweed, and some were also more strongly associated with seagrass. Thus, although tropical and temperate species inhabit the same location, their overlap decreases at finer spatial scales (Streit, Cumming, & Bellwood, 2019). Moreover, specific feeding behaviours can also increase niche dissimilarity among species; for instance, species that tend to feed on drifting macrophytes, such as *S. fuscescens*, reduce resource competition in the benthic space (Zarco-Perello et al., 2019). Hence, there seem to be ample niche spaces available in temperate ecosystems for range-shifting tropical herbivores to occupy, without directly competing against their temperate counterparts (Vergés et al., 2019).

The addition of tropical herbivorous fish to temperate ecosystems changed the spatial patterns of functional diversity, functional uniqueness and the intensity of specific herbivory functions in our study. Changes in species richness caused by climate change have been forecast and described by multiple studies, with tropical regions expected to suffer losses in biodiversity, while temperate regions are likely to experience increases in species richness that could modify ecological processes (Blowes et al., 2019). Our results expanded on this from a functional perspective, showing that the expansion of tropical species to temperate ecosystems could initially lead to general increases in functional diversity (FD) at sites where they establish permanent and abundant populations. This can lead to increases in functional redundancy but also to the introduction of new herbivory functions. The low number of temperate species per herbivory function implies that some functions are not performed at many sites, and that the arrival of tropical species could fill these empty functional niches. This explains the increase in functional uniqueness (*U*) that we observed in subregions where tropical herbivores had established. However, increments were heterogeneous in space depending on how functionally redundant tropical ensembles were in relation to the temperate communities they overlapped with.

While increments in FD were similar between Rottnest Island and North Perth (24% and 33%), the increment in U was double in the latter (47% vs. 109%). This shows that there was a higher redundancy of functions at Rottnest Island, and conversely that there were more sites in North Perth where rabbitfish brought new functions (Ricotta et al., 2016). Among these, seagrass browsing seemed to be the main driver of change, since it was the only function that increased significantly in spatial extent and up to 3× and 32× more in intensity than seaweed grazing and browsing in North Perth and Rottnest Island respectively. This is understandable since only the trumpeter *Pelates octolineatus* has been identified as an important temperate seagrass consumer (Bessey & Heithaus, 2015), reflecting historically low rates of herbivory in seagrass meadows of the region (White, Westera, & Kendrick, 2011).

Knowledge of the baseline abundance and functional role of herbivorous species in recipient ecosystems is crucial to accurately assess and forecast changes in functional processes under tropicalization. While tropical species drove increases in all functions, the total intensity was strongly determined by the native temperate assemblages. From a species diversity perspective, Rottnest Island is the most tropicalized subregion of south-western Australia, being the only one hosting both rabbitfish and parrotfish. Nonetheless, from a functional perspective it had similar diversity to Geographe Bay, and substantially lower functional diversity than North Perth, owing to the more diverse temperate communities in those regions prior to the addition of tropical rabbitfish. Likewise, Rottnest Island experienced by far the highest increase in seagrass browsing intensity but maintained similar overall mean values to other subregions not hosting tropical species. Additionally, seaweed browsing and grazing increased the most in North Perth, but overall Rockingham had similar levels for the former and Rottnest Island for the latter, since both had strong temperate communities in these functions.

The fact that the average intensities of seaweed browsing were similar between some tropicalized and non-tropicalized areas indicates that consumption rates in the region have not yet reached levels that pose a significant risk of regime-change at extensive spatial scales. However, shifts could occur in the future as tropical herbivores further expand their distribution and abundance in temperate ecosystems. High densities of tropical herbivores at local spatial scales have been correlated with increases in herbivory, declines in biomass of kelp (Zarco-Perello et al., 2017) and the maintenance of canopy-free states and high turf cover following environmental disturbances, resulting in a positive feedback loop that favours the persistence of tropical herbivores and decreases the seascape resilience of temperate ecosystems (Bennett et al., 2015). This is consistent with ecological theories indicating that ecosystem processes are strongly determined by the abundance of species with high importance in certain ecological functions (Mokany, Ash, & Roxburgh, 2008). Species composition and dominance within ecosystems are therefore likely to be highly significant, and the impact of the tropicalization of herbivorous communities could be driven in great part by the expansion of keystone species of tropical herbivores (Hoey & Bellwood, 2009), in combination with the establishment of abundant populations of other species with lower impact per capita (Ruttenberg et al., 2019).

Our study shows empirically how range-shifting tropical species can affect herbivory in temperate habitats across large spatial extents. The high overlap with temperate species that we observed is not surprising considering that tropical coral reefs have fewer macrophyte resources shared among a higher number of species and populations than temperate ecosystems do. Consequently, we can expect that resource limitation in the form of space and food will not constrain further tropicalization of temperate ecosystems under climate change, with reefs with high turf cover and seagrass meadows facilitating the range-expansion and persistence of tropical fish in temperate regions. By assessing novel species interactions in three levels of overlap between temperate herbivores, tropical herbivores and temperate macrophytes, we found that in a first stage of tropicalization, temperate marine ecosystems will experience increases in the diversity, intensity and spatial extent of different herbivory functions as tropical species with different habitat affinities, feeding behaviours and diets shift their distribution poleward. Functional redundancy will be heterogeneous and might not necessarily increase initially in many sites due to the low abundance and diversity of herbivory functions in some temperate ecosystems, but it will likely do so more broadly as further tropical species arrive, their abundance increase and both the spatial and functional overlap of the communities rise.

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AUTHORS' CONTRIBUTIONS

S.Z.-P. conceived the study; S.Z.-P. and T.W. acquired the funding; S.Z.-P. collected the field data; S.Z.-P. and G.C. analysed the data; S.Z.-P. wrote the paper and all authors contributed to drafting the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.8w9ghx3hx (Zarco-Perello & Wernberg, 2020).

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SUPPORTING INFORMATION

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

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