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CORAL REEF FUNCTIONAL ECOLOGY IN THE ANTHROPOCENE

Form and function of tropical macroalgal reefs in the Anthropocene

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Abstract

1. Tropical reefs have been subjected to a range of anthropogenic pressures such as global climate change, overfishing and eutrophication that have raised questions about the prominence of macroalgae on tropical reefs, whether they pose a threat to biodiversity, and how they may influence the function of tropical marine ecosystems.
2. We synthesise current understanding of the structure and function of tropical macroalgal reefs and how they may support various ecosystem goods and services. We then forecast how key stressors may alter the role of macroalgal reefs in tropical seascapes of the Anthropocene.
3. High levels of primary productivity from tropical canopy macroalgae, which rivals that of other key producers (e.g., corals and turf algae), can be widely dispersed across tropical seascapes to provide a boost of secondary productivity in a range of biomes that include coral reefs, and support periodic harvests of macroalgal biomass for industrial and agricultural uses. Complex macroalgal reefs that comprise a mixture of canopy and understorey taxa can also provide key habitats for a diverse community of epifauna, as well as juvenile and adult fishes that are the basis for important tropical fisheries.
4. Key macroalgal taxa (e.g., *Sargassum*) that form complex macroalgal reefs are likely to be sensitive to future climate change. Increases in maximum sea temperature, in particular, could depress biomass production and/or drive phenological shifts in canopy formation that will affect their capacity to support tropical marine ecosystems.

5. Macroalgal reefs can support a suite of tropical marine ecosystem functions when embedded within an interconnected mosaic of habitat types. Habitat connectivity is, therefore, essential if we are to maintain tropical marine biodiversity alongside key ecosystem goods and services. Consequently, complex macroalgal reefs should be treated as a key ecological asset in strategies for the conservation and management of diverse tropical seascapes.

KEYWORDS
nursery, productivity, *Sargassum*, seascape, seasonality, spatial subsidy

1 | INTRODUCTION

Tropical macroalgal reefs, which we define as patches of carbonate reef with higher relative cover of fleshy macroalgae than live coral, have long been recorded alongside coral and other patch habitat types in a range of fringing, barrier and atoll reef settings (Bruno, Precht, Vroom, & Aronson, 2014; Littler & Littler, 1988; Stephenson, Stephenson, Tandy, & Spender, 1931). Some types of tropical macroalgae have been increasing in prevalence during the Anthropocene due to overfishing, coral bleaching and/or eutrophication removing some of the limitations to macroalgal growth on tropical reefs, which in some cases has triggered broad-scale coral–algal regime shifts (e.g., Hughes, 1994; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). While this has increased awareness of macroalgae in tropical reef research and management, this has often been skewed towards the negative effects of macroalgae on coral reefs (e.g., Bellwood, Hughes, Folke, & Nyström, 2004; Hughes et al., 2017). However, macroalgae can be the dominant benthic organism on tropical reefs due to a range of environmental drivers (Bruno et al., 2014; Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015), and as primary producers that span a range of growth forms, macroalgae have the capacity to support many other species in tropical marine ecosystems (Fulton et al., 2014; Tano et al., 2016). Moreover, seascape-scale assessments of shallow tropical waters indicate areas of macroalgal reef (e.g., 16%, 23% and 46% in Tanzania, New Caledonia and Ningaloo, respectively) can be extensive relative to coral-dominated habitat (4%–8%; Garrigue, 1995; Kobryn, Wouters, & Beckley, 2011; Tano et al., 2017). Depending on the spatial setting and extent, macroalgal reefs can be key components of interconnected tropical seascapes that complement the functions and services provided by other subtidal habitats, such as coral reefs and seagrass beds (Hyndes et al., 2014; Nagelkerken, Sheaves, Baker, & Connolly, 2015).

Macroalgal reefs vary immensely in composition and structure in response to a range of environmental and biotic conditions (Steneck & Dethier, 1994). In some settings, a tropical reef can become dominated by a few weedy macroalgae species of low stature, especially when grazing pressure is severely depressed by overfishing (e.g., Littler & Littler, 1988; Hughes, 1994; Mumby, 2009). However, macroalgae can also dominate tropical reefs where natural levels of wave energy, sedimentation and nutrient supply facilitate macroalgal growth over that of benthic competitors such as corals and coralline algae (Bruno et al., 2014; Gove et al., 2015; Williams et al., 2015). Under these conditions, complex macroalgal reefs have developed across the Indo-Pacific and Red Sea, where they typically comprise a mixture of canopy-forming (e.g., *Sargassum* and *Turbinaria*) and/or understorey taxa (e.g., *Dictyota* and *Lobophora*) that provide microhabitats for a diversity and abundance of epifauna and nekton (Ateweberhan, Bruggemann, & Breeman, 2006; Rossier & Kulbicki, 2000; Tano et al., 2016). Such macroalgae-associated fauna also take advantage of the local productivity to fulfil their trophic requirements—either directly as herbivores or indirectly as carnivores exploiting secondary production (Edgar & Aoki, 1993; Lim, Wilson, Holmes, Noble, & Fulton, 2016; Wenger, van Lier, & Fulton, 2018). In this way, macroalgal reefs can facilitate biodiversity and flows of energy and biomass to underpin a range of tropical marine ecosystem goods and services (Figure 1).

In this review, we synthesise our current understanding of how the structure and function of macroalgal reefs can influence the services they support within tropical marine ecosystems. We then explore how environmental stressors interact with these macroalgal structure–function relationships and what this means for the future of tropical reefs in the Anthropocene. In doing so, we challenge some emerging paradigms and reappraise how we should manage tropical macroalgal reefs as part of diverse and connected seascapes.

2 | ECOSYSTEM FUNCTIONS AND SERVICES FROM MACROALGAL REEFS

2.1 | Primary and secondary production

Productivity is a fundamental attribute of ecosystems that influences overall patterns of biodiversity, structure and function, and the extent of goods and services that can be sustained over space and time. Our meta-analysis of areal productivity across a range of common benthic producers (i.e., taxa that typically comprise 10% or more of the benthic cover on tropical reefs) indicated high rates of both gross and net areal primary production in two key groups—reef-building corals and canopy-forming *Sargassum*—both of which also provide habitat for other species (Figure 2a). Net production from *Sargassum* is typically rapid and episodic, with an almost complete

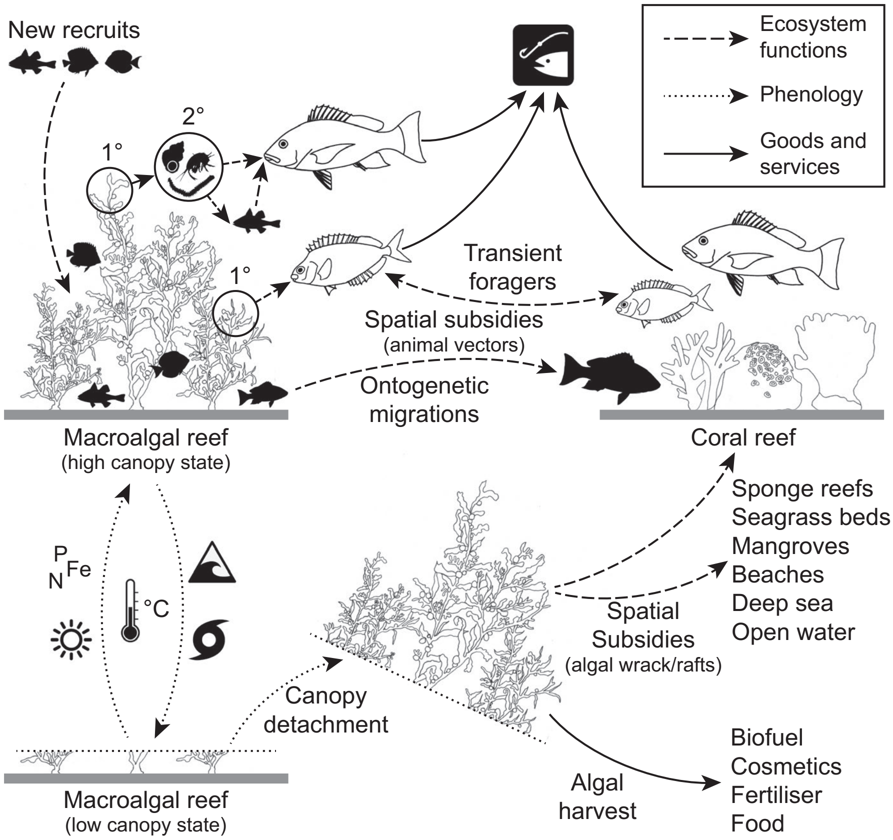

FIGURE 1 How complex tropical macroalgal reefs can support marine ecosystem functions, goods and services. Seasonal cycles in the phenology of canopy-forming macroalgae (e.g., *Sargassum*) provide primary (1°) and secondary (2°) production as well as habitat for resident and transient consumers, especially during high canopy states. Spatial subsidies of macroalgal productivity to other biomes occur via surface (rafts) and subsurface (wrack) dispersal of detached macroalgal canopy biomass and faunal migrations. The timing and extent of these phenological cycles in tropical macroalgal canopy biomass, which underpin food security and other harvest products, are dependent on several environmental drivers such as sea temperature, daylength, nutrient pulses and disturbance events (Figure 2)

annual turnover of biomass across seasonal cycles of canopy growth and decay (Figure 2b). Similar seasonal variation in the productivity of other reef producers is likely due to shifts in daylength and sea temperature (Kinsey, 1977), although the short time periods of most production estimates (hours/days) prevent a wider investigation of seasonal variation in tropical reef production. Once detached, macroalgal canopy biomass is widely dispersed by drifting rafts and wrack, which can be deposited across a range of subtidal and intertidal biomes (Figure 1; Section 2.3).

Consumption and conversion of primary production into higher trophic levels are critical for many ecosystem goods provided by tropical reefs, such as fishable biomass. In corals, much of the relatively high net primary production from zooxanthellae is utilised by the host coral (Hatcher, 1990), with feeding by corallivores and coral exudates providing external trophic pathways for some of the coral primary production to enter the wider ecosystem (Cole, Lawton, Wilson, & Pratchett, 2012; Wild et al., 2004). However, another major component of coral-dominated reefs, the epilithic algal matrix (EAM), is known to support high levels of net primary production that is readily converted into herbivorous fish biomass (Bellwood et al., 2018; Russ, 2003). Similarly, a number of herbivorous fishes such as *Leptoscarus vaigiensis*, *Siganus sutor* and *Naso unicornis* have evolved to target the high net primary production of canopy-forming macroalgae (Choat, Robbins, & Clements, 2004; Hoey, Brandl, & Bellwood, 2013; Lim et al., 2016). These browsing herbivores may exhibit some of the highest known rates of secondary production (i.e., somatic growth) in tropical reef fishes (Morais & Bellwood, 2018), which can underpin important tropical fisheries (Hicks & McClanahan, 2012; Robinson et al., 2018; Rogers, Blanchard, & Mumby, 2018). We note emerging evidence that suggests microalgae, endolithic algae and bacteria are targeted by some reef fishes (Clements et al., 2017), which further quantitative data may ultimately reveal as a highly productive resource alongside macroscopic autotrophs such as macroalgae and corals.

Canopy macroalgae can also facilitate secondary and higher order productivity through their epifauna. *Sargassum* and other macroalgae with complex canopies can host a wide diversity and abundance of invertebrate epifauna, which in turn support the growth and reproductive output of carnivorous fishes that target these epifaunal prey (Edgar & Aoki, 1993; Wenger et al., 2018). Indeed, macroalgal reefs appear to host a greater diversity and higher standing biomass of epifauna than either tropical seagrass (Tano et al., 2016) or the EAM (e.g., crustacea; Kramer, Bellwood, & Bellwood, 2014), which is likely due to the higher (volumetric) capacity for canopy-forming macroalgae to support epifauna than other types of smaller macrophyte host (Wenger et al., 2018). This means canopy-forming macroalgae can support secondary productivity an order of magnitude higher than EAM or many other types of subtidal microhabitat, with the exception of dead coral heads that may also provide complex “canopy” habitat for epifauna (Edgar, 1990; Edgar & Aoki, 1993; Kramer et al., 2014). Consequently, tropical macroalgae can be both key primary producers and facilitators of secondary production that underpin major trophic flows of energy and biomass through tropical marine ecosystems.

2.2 | Complex habitat for key species and processes

Habitat complexity is integral for maintaining the biodiversity of tropical reefs. The collapse of coral reef structural complexity is associated with a substantial loss of reef-associated species (Graham & Nash, 2013; Rogers, Blanchard, & Mumby, 2014). Macroalgal habitats have similar functional relationships with their associated biota, where changes in canopy structure (density, cover, height) and composition are strong predictors of the abundance and diversity of key epifauna and nekton (Tano et al., 2016; Wenger et al., 2018; Wilson et al., 2014). While there appear to be relatively few macroalgal reef specialist fishes (Rossier & Kulbicki, 2000), many tropical reef fish taxa are supported as transients across macroalgal and coral reef habitats during ontogeny or foraging migrations (Figure 1). Notably, macroalgal-associated fishes span a diversity of trophic groups, albeit at a lower level of taxonomic diversity and redundancy than those found on coral reefs (Figure 3). Nonetheless, many of the relatively abundant macroalgal-associated fish taxa are of ecological significance, such as browsing herbivores (e.g., *Leptoscarus vaigiensis*, *Siganus sutor*), generalist carnivores (e.g., *Lethrinus* spp.) and piscivores (e.g., *Epinephelus* spp.), many of which are also important fishery targets (Hicks & McClanahan, 2012; Robinson et al., 2018; Rossier & Kulbicki, 2000; Wilson et al., 2017).

Habitat quality and complexity are also critical for supporting key ecosystem processes. Complex macroalgal reefs comprising canopy-forming genera like *Sargassum* can play a major role in supporting the replenishment of fish populations via the provision of seasonal nursery habitats for juveniles (Figure 3a). Our meta-analysis revealed that 17%–49% of the regional pool of reef fish species have the majority of their juveniles within complex macroalgal reef habitats (Supporting Information Table S3)—around three-quarters of those taxa later migrate to coral reefs where the majority of their adults are found (Figure 3a). Importantly, variations in macroalgal canopy structure are closely linked to the diversity and abundance of juvenile fishes occupying a particular patch (Wilson et al., 2014) and the abundance of future life-history stages (Figure 3b; Aburto-Oropeza, Sala, Paredes, Mendoza, & Ballesteros, 2007; Wilson et al., 2017). Consequently, local changes in macroalgae canopy habitat can influence the number of juveniles that recruit into future adult fish populations, including those which are prime fishery targets in coral reef habitats. Accordingly, macroalgal-dominated reefs can underpin both the replenishment and productivity of tropical reef fisheries.

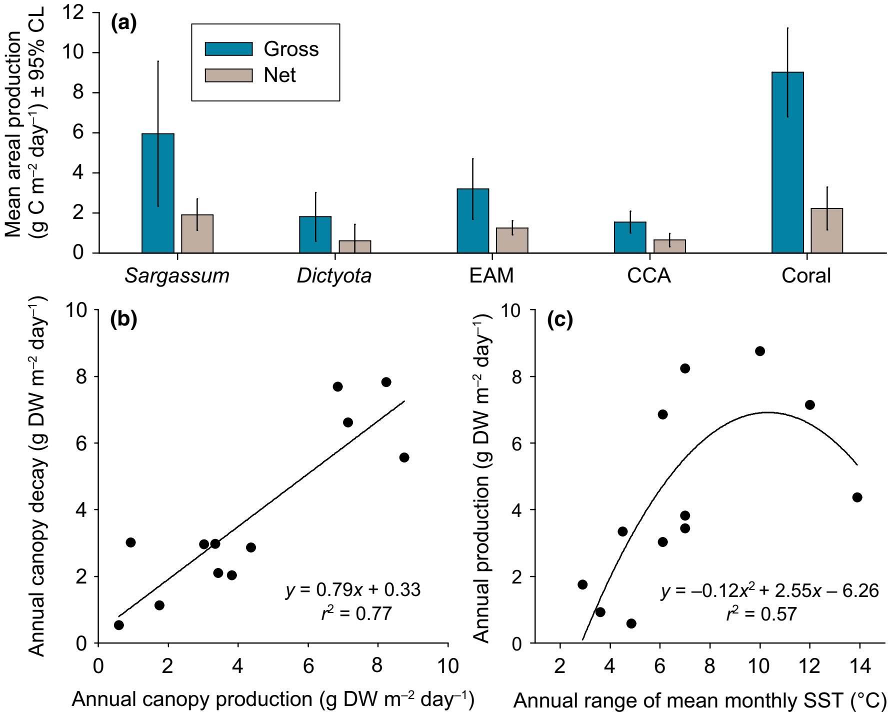

FIGURE 2 Comparison of (a) mean gross and net areal production in sections of tropical reef dominated by one of five major primary producers—canopy-forming *Sargassum*, *Dictyota*, the epilithic algal matrix (EAM), crustose coralline algae (CCA) or scleractinian corals—based on 40 independent studies at tropical locations (see Supporting Information Table S1). Means (± 95% confidence limits) are based on four or more studies per group (except *Dictyota* gross production where $n = 2$, Supporting Information Table S1). Note that net production for *Sargassum* was typically measured on uncaged biomass (i.e., subject to herbivory) during the seasonal growth phase (typically 4–6 months), which is followed by 3–4 months of canopy detachment when 80%–90% of production is dispersed. As such, production values are likely to be conservative for macroalgae due to losses from herbivory (Poore et al., 2012). Meta-analysis of relationship between (b) in situ annual growth and decay of tropical *Sargassum* canopy biomass, and (c) in situ annual *Sargassum* canopy growth and the annual range in mean monthly sea surface temperatures (SST) recorded by 12 independent studies focused on *Sargassum*-dominated reef areas at seven tropical locations (Supporting Information Table S2)

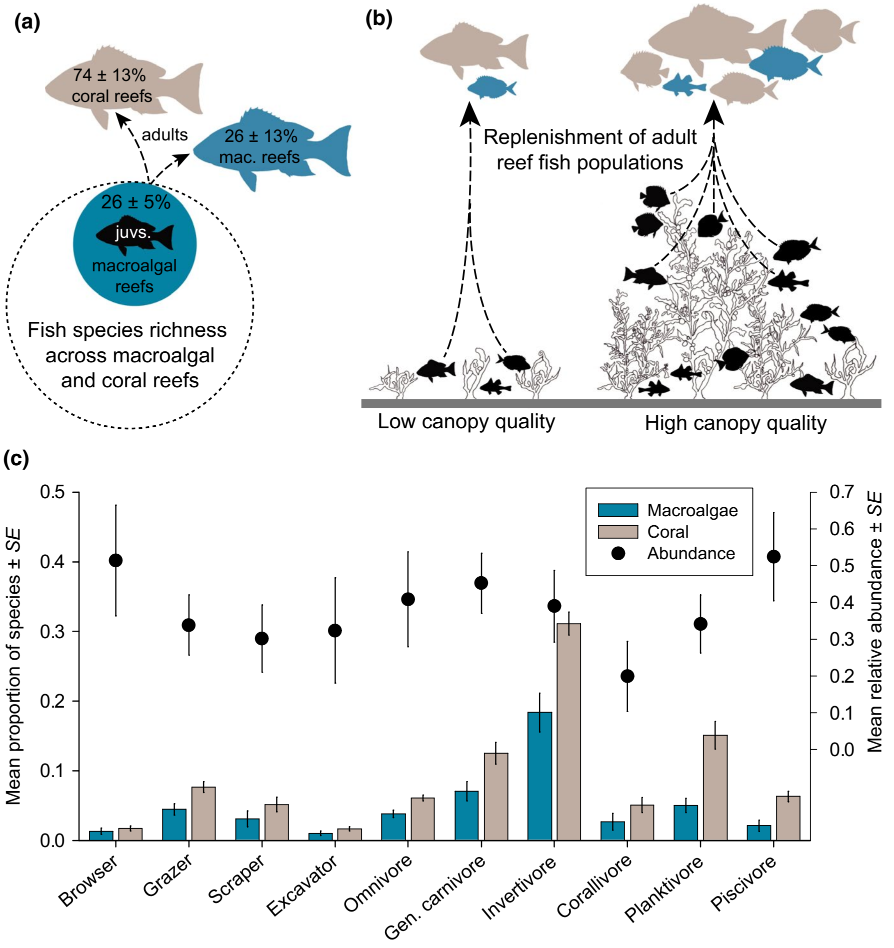

FIGURE 3 Role of complex macroalgal reefs in supporting tropical fishes via: (a) dominant habitat for the juvenile stages of 26% ± 5% (mean ± *SE*) of local reef fish species occurring across macroalgal and/or coral reefs—the adults of most of these species (74% ± 13%) are predominantly found on coral reefs (underlying meta-data in Supporting Information Table S3); (b) complex habitat for juvenile reef fishes, where canopy habitat quality (per cent cover, density, canopy height) can strongly influence the diversity and abundance of new fish recruits that survive to replenish adult populations in both coral (grey) and macroalgal (blue) reefs, including fishery target species; and (c) supporting a diverse community of adult reef fishes that is comparable to nearby coral reefs, yet at much lower levels of taxonomic redundancy (Supporting Information Table S4). Note the mean relative abundance of species (>0.5 equates to more individuals on macroalgal than coral reef) in these trophic groups (dots, right y-axis) is around 0.5 or below, which suggests most adult reef fishes are not specialised occupants of complex macroalgal reefs, and likely use such areas as transient foraging grounds (e.g., browsers and piscivores)

2.3 | Spatial subsidies across tropical seascapes

Spatial subsidies occur when there is a decoupling between the location of primary production and where the biomass and energy are assimilated. The rapid seasonal accumulation and subsequent detachment of tropical *Sargassum* canopy biomass create a pathway for this energy and nutrients to be widely dispersed to other marine ecosystem components via rafting (Zubia, Andréfouët, & Payri, 2015), underwater wrack and movement of transient fauna (Hyndes et al., 2014; Polis, Anderson, & Holt, 1997). Direct transport of biomass can be considerable depending on the dispersal vector. On tropical reefs, drift biomass derived from tropical *Sargassum* has been recorded at a rate of 20.8 g C m^{-2} day^{-1} across Hawaiian coral reefs (Morrisey, 1985 in Stimson, 2013), while at depths of 40 metres macroalgal biomass arrives on reef slopes at rates of 2.5 g C m^{-2} day^{-1} (Stimson, 2013). Such spatial subsidies of macroalgal biomass are substantial, being more than double the in situ areal production of other common tropical benthic organisms (Figure 2a). Macroalgal wrack and rafts are then likely to enter detrital pathways and fuel secondary production in areas where it is deposited (Hyndes et al., 2014; Wilson, Bellwood, Choat, & Furnas, 2003).

Macroalgae-derived energy and nutrients can flow throughout tropical marine ecosystems via various pathways. For instance, macroalgae exudates (dissolved organic carbon) are rapidly taken up by sponges and their associated bacteria, which is then passed to corals and higher trophic levels via the sponge-detritus loop (Mumby & Steneck, 2018; Rix et al., 2017). Mobile animals may also transport production that was consumed in macroalgal reefs over considerable areas and distances via predator–prey linkages and excretion of wastes across the seascape (Berkström et al., 2012). For instance, the diurnal foraging migrations of large-bodied carnivorous reef fishes can cover ranges of up to 1,300 hectares that encompass both coral and macroalgal reefs (Babcock, Pillans, & Rochester, 2017; Taylor & Mills, 2013). Likewise, ontogenetic migrations of fish that live and feed on macroalgal reefs as juveniles can transfer macroalgal productivity across seascapes over much longer time-scales. Through these mechanisms, the high primary production within macroalgal reefs becomes dispersed across habitats to support whole-ecosystem productivity that is critical for maintaining biodiversity and food security.

2.4 | Industrial products and solutions

Wild and cultivated tropical macroalgae are currently harvested for industrial products that include food, biofuel, cosmetics, pharmaceutical compounds, agricultural products and antifouling compounds (Borines, McHenry, & de Leon, 2011; Prud'homme van Reine & Trono, 2001; Song, Duc Pham, Seon, & Chul Woo, 2015). Much of this harvest of tropical macroalgae occurs in South-East Asia and East Africa, but it has the capacity to support coastal livelihoods throughout the Indo-Pacific (Borines et al., 2011; Prud'homme van Reine & Trono, 2001). The phenology and high productivity of tropical taxa such as *Sargassum* facilitate sustainable annual harvests of high areal yield (Zubia et al., 2015). Indeed, this potential for high productivity is a reason why tropical macroalgae have been suggested as a vector for carbon sequestration (Chung, Beardall, Mehta, Sahoo, & Stojkovic, 2011; Sondak et al., 2017). Emerging evidence indicates that macroalgal reefs have the capacity to store "blue" carbon via burial in adjacent sediment deposits and/or transport into the deep sea (Atwood et al., 2018; Krause-Jensen & Duarte, 2016). However, for carbon capture and storage to be of significant magnitude relative to global carbon emissions, rates of production need to be increased. Given nutrient availability is a key limitation (Littler, Littler, & Titlyanov, 1991; Roff & Mumby, 2012), the addition of micronutrients has been suggested as one way to boost carbon capture by marine primary producers such as phytoplankton (Bigg, Jickells, Liss, & Osborn, 2003). However, such micronutrient augmentation can have unintended effects and may not produce negative carbon emissions after nutrient fabrication and transport are taken into account. Moreover, micronutrient additions (e.g., iron) can increase the prevalence of undesirable ecosystem components such as cyanobacterial mats (Kelly et al., 2012). Perhaps more feasible is the direct capture of carbon dioxide from industrial activities (e.g., ethanol production) to fuel tropical macroalgae mariculture that is converted into forms for long-term carbon storage (e.g., biochar; Roberts, Paul, Dworjanyn, Bird, & de Nys, 2015).

3 | FUTURE SCENARIOS FOR MACROALGAE IN TROPICAL SEASCAPES

What will be the nature and function of macroalgae in tropical seascapes of the future? To answer this question, we must explore the proximate effects of global and local stressors on the composition of macroalgal reefs, their productivity and their likely context within tropical seascapes. Marine climate change in the form of ocean warming, acidification and/or shifting storm regimes may impinge on tropical macroalgal reef structure and function. Of particular concern are thermal anomalies that are likely to intensify in tropical marine regions if we continue on "business-as-usual" scenarios (van Hooidonk et al., 2016; Oliver et al., 2018). Current evidence indicates that annual canopy production in a key taxon—*Sargassum*—is sensitive to thermal climate, both in terms of mean sea surface temperature (SST; Glenn, Smith, & Doty, 1990; Ateweberhan et al., 2006; Fulton et al., 2014), and the annual range in mean monthly SST (Figure 2c). While intermediate levels of ocean warming might increase macroalgal growth and production in some understorey taxa such as *Laurencia* and *Lobophora* (Gouvea et al., 2017; Hernández, Sangil, Fanai, & Hernández, 2018), this may not be the case for canopy-forming *Sargassum* that exhibit lower levels of canopy biomass at upper extremes of regional SST (Ateweberhan et al., 2006; Fulton et al., 2014; Hwang, Tsai, & Lee, 2004). This may be because these canopy-forming macroalgae, like many other tropical species, are already living close to their thermal limits (Koch, Bowes, Ross, & Zhang, 2013). Indeed, the available evidence suggests anomalies of 1–2°C above the highest mean monthly SST are likely to cause severe declines in *Sargassum* growth and canopy collapse (McCourt, 1984; Prince, 1980). However, understorey fleshy macroalgae may exhibit either resistance (no effect) or a modest increase in production under combinations of warming and acidification (Gouvea et al., 2017; Hernández et al., 2018; Johnson, Price, & Smith, 2014). Taken collectively, this suggests marine climate change will drive a loss of tropical canopy-forming taxa to effectively flatten macroalgal reefs down to low-complexity stands of short and/or unpalatable macroalgae (Littler & Littler, 1988; Littler et al., 1991).

In the near term, a shift in the composition and canopy structure of macroalgal reefs will have major consequences for tropical ecosystems. The implications for productivity are obvious in that less canopy growth will mean a decline in the annual turnover and dispersal of primary production across our tropical seascapes, followed by declines in secondary and higher-level production. The consequences of macroalgal habitat degradation could also be substantial for key biota such as fishes. This is because of the strong functional links between macroalgal habitat quality and reef fish abundance, particularly canopy height and density, which are sensitive to variations in sea temperature over annual and interannual (Fulton et al., 2014) and longer (Wilson et al., 2018) temporal cycles. In years of poor canopy growth, we tend to find a lower abundance and diversity of juvenile and adult fishes on macroalgal reefs (Aburto-Oropeza et al., 2007; Wilson et al., 2018), which can translate to smaller future fish populations on both macroalgal and coral reefs (Wilson et al., 2017). These effects are particularly severe for species that are macroalgal reef specialists (Lim et al., 2016; Wenger et al., 2018), but they can also impact the many species that predominantly settle into macroalgal reefs.

Fishes that recruit to macroalgal reefs may be particularly vulnerable to shifts in canopy phenology arising from climate change. On "hot reefs" with very high summer maximum SST (e.g., 35°C in Red Sea and southern Taiwan), peak *Sargassum* canopy biomass occurs in the cooler winter–spring period (Ateweberhan et al., 2006; Hwang et al., 2004), rather than the summer–autumn at most other tropical locations (Fulton et al., 2014; Glenn et al., 1990; Vuki & Price, 1994). Global increases in summer maximum SST due to climate change may drive a general shift in *Sargassum* canopy phenology towards the "hot reefs" condition (i.e., peak during cooler winter months), which would create a nursery habitat mismatch for the many fish species that exhibit summer peaks in recruitment (Abesamis & Russ, 2010; McIlwain, 2003; Williams, 1983). An adaptive shift in fish recruitment season is possible, with indications that reef fishes recruiting to "hot" macroalgal reefs mostly do so during the cooler months when *Sargassum* canopy biomass is highest (Isari et al., 2017). Such recruitment patterns can arise from seasonal shifts in the survival of juveniles, rather than shifts in spawning behaviour and reproductive output (Robertson, 1990), which means taxa with more serial recruitment patterns (e.g., some Acanthurids, Labrids, Haemulids and Pomacentrids; Doherty, 1991; Srinivasan & Jones, 2006; Sponaugle, Walter, Grorud-Colvert, & Paddack, 2012) may be more adaptable to shifts in macroalgal habitat phenology.

Many of the ecological functions of macroalgal reefs depend on connectivity across a mosaic of reef types, so seascape context is critically important for understanding future scenarios for tropical reefs. Catastrophic declines in coral cover have become prevalent in the Anthropocene and are predicted to accelerate during this century (Hughes et al., 2018). A substantive loss of either macroalgal or coral cover will break pathways of connectivity that are integral for sustaining biodiversity via ontogenetic and foraging migrations (Harborne et al., 2016; van Lier, Wilson, Depczynski, Wenger, & Fulton, 2018), and spatial subsidies that underpin productivity and harvestable biomass. A loss of reef-building corals and crustose coralline algae will also jeopardise the carbonate reef base required for all types of tropical reef (including macroalgal) and their associated biota. The spatial scales at which such seascape connectivity may be broken are alarmingly small. For one of the main vectors—reef fishes—van Lier et al. (2018) found marked reductions in fish diversity (taxonomic and functional) on macroalgal reefs when the distance between coral and macroalgal patches exceeded 500 m. Similarly, Berkström, Lindborg, Thyresson, and Gullström (2013) found 750 m to be a key threshold for the abundance of adult reef fishes that are transient foragers across a mosaic of tropical habitats (coral, seagrass and macroalgae). These distance thresholds are likely to be much lower for juvenile fishes undertaking ontogenetic migrations (Berkström et al., 2013; Grober-Dunsmore et al., 2008). Moreover, key processes such as grazing activity by transient herbivorous fishes may also be substantially affected at small spatial scales of patch separation (e.g., 75–100 m; Vergés, Vanderklift, Doropoulos, & Hyndes, 2011; Downie, Babcock, Thomson, & Vanderklift, 2013). Seascapes must comprise a mix of coral and macroalgal reefs, as well as other habitat types, to support the complement of species that underpin the ecological processes and connections that maintain healthy and productive tropical ecosystems.

With mass coral bleaching and mortality increasing world-wide, we are entering an era of increasing dominance of tropical reefs by organisms other than coral. Many coral reefs comprise a mix of coral and algal cover (mostly as an epilithic algal matrix or EAM; Bruno et al., 2014; Goatley & Bellwood, 2011), which sustains a diverse and productive fish fauna of grazers, detritivores and carnivores (Bellwood et al., 2018; Rogers et al., 2018; Russ, 2003; Wilson et al., 2003). Reefs dominated by a mix of understorey and canopy-forming macroalgae can have a similar diversity of fish trophic groups, although at a lower level of species richness (Figure 3c). Indeed, fish communities on reefs that have undergone regime shifts from coral to canopy-forming macroalgae have shown such changes in functional structure, yet they are still diverse and abundant (Graham et al., 2015). Moreover, many of the fishes that utilise complex macroalgal reefs can support productive fisheries (Hicks & McClanahan, 2012; Robinson et al., 2018). However, it is conceivable that future coral–algal regime shifts may occur when environmental conditions are unsuitable for canopy-forming macroalgae like *Sargassum*. If the thermal anomalies that have triggered mass bleaching and mortality of corals world-wide (Hughes et al., 2018) continue to increase in severity and frequency (van Hooidonk et al., 2016; Oliver et al., 2018), then we may also see a collapse of canopy-forming macroalgae in many tropical regions. This means that with continuing ocean warming, the future for an increasing number of tropical reefs may be one where two key habitat-forming groups—corals and canopy-forming macroalgae—are no longer able to sustain the productive and complex habitats that underpin key ecological functions and socio-economic benefits. Instead, we could see a greater dominance of macroalgae that have lower levels of structural complexity (e.g., EAM), lower areal productivity (e.g., *Dictyota*; Figure 2a) and/or low palatability (e.g., *Turbinaria*; Bittick, Bilotti, Peterson, & Stewart, 2010). These types of macroalgal reef state will not support the same spectrum of ecosystem functions we have come to expect from diverse and productive tropical seascapes comprising coral, canopy-forming macroalgae and other complex reef habitats.

4 | RESEARCH AND MANAGEMENT PRIORITIES

Tropical reefs are imperilled by a range of threats that have increased the risk and extent of coral–algal regime shifts around the world during the Anthropocene (Bellwood et al., 2004; Graham et al., 2015; Hughes et al., 2017). Wholesale shifts from coral to macroalgal-dominated states are an example of the negative effects of macroalgal overgrowth. However, macroalgae do have important roles to play in tropical marine ecosystems. Tropical macroalgal reefs are common in proximity to landmasses (Littler et al., 1991), where they can be one of the most prominent types of shallow-water habitat (Garrigue, 1995; Kobryn et al., 2011; Tano et al., 2017). This creates a risk of erroneously concluding that macroalgal-dominated areas are largely due to anthropogenic impacts such as eutrophication and overfishing. A key criterion for classifying a state of algal overgrowth should be evidence that a coral–algal regime shift has occurred, concomitant with feedback processes (e.g., reduced herbivory) that maintain a skew towards macroalgal reef states (Bellwood et al., 2004; Scheffer & Carpenter, 2003). In such circumstances, the key stressors should be identified and directly addressed in an attempt to promote recovery to a pre-regime shift state. However, if such evidence is lacking, then we cannot exclude the possibility that macroalgal-dominated habitats are a natural component of the tropical seascape (Bruno et al., 2014; Gove et al., 2015; Williams et al., 2015). Indeed, macroalgal reefs are found along coastlines and on remote reefs with relatively low anthropogenic impacts relevant to macroalgal growth (i.e., minimal land-use and catchment modifications, and minimal harvest of herbivores), where they are part of an interconnected mosaic of coral and other patch habitat types (e.g., Kobryn et al., 2011; Gove et al., 2015; Williams et al., 2015). In such cases, macroalgal reefs may warrant protection to support their key roles in ecosystem productivity and function.

Macroalgal reefs can vary immensely in their capacity to support ecosystem functions, goods and services. High-complexity macroalgal reefs comprising a mixture of canopy and understorey taxa have the potential to support biodiversity and productivity at many levels, including key fisheries that underpin food security for tropical maritime nations. We suggest there is sufficient evidence to include complex macroalgal reefs as a key habitat within a mosaic of "seascape nurseries" (Harborne et al., 2016; Nagelkerken et al., 2015) that warrant attention in conservation and spatial management strategies. Evidence is also building that complex macroalgal reefs may be instrumental in supporting productivity across the tropical seascape via spatial subsidies, and in so doing, support a broad range of ecosystem goods that span direct algal harvests to enhanced levels of fishable biomass. Given the potential for wide variations in canopy quality and biomass turnover, and the functional consequences for the role of macroalgal reefs in tropical marine ecosystems, there is a need to identify and protect high-quality patches from local threats. The latter include increases in turbidity, habitat destruction from anchoring, sediment smothering from poor catchment management and dredging (Umar, McCook, & Price, 1998), as well as overfishing-induced trophic cascades that drive the ecological release of herbivores (e.g., urchins; Wallner-Hahn et al., 2015).

Given the vast differences in the emergent ecosystem functions that can arise from different types of macroalgal reefs, identifying the environmental thresholds that may bound different macroalgal reef states is a high priority. Low-complexity macroalgal reefs, such as those typical of the early stages of a coral–algal regime shift under high anthropogenic stress, are unlikely to support high levels of marine biodiversity and ecosystem function. Yet, there is a strong potential for these types of macroalgae to dominate tropical reefs of the Anthropocene. Since so many ecosystem functions flow from canopy structure and turnover, we also need to assess how environmental change may affect tropical macroalgal phenology (Koch et al., 2013). In part, this means a better understanding of the resilience of different macroalgal reef types to disturbance such as unseasonal canopy loss from storms and marine heatwaves, and their resistance to long-term stressors such as sedimentation and climate change. Indeed, more information on the thermal thresholds that will trigger shifts in the timing and extent of macroalgal canopy production and decay should be a priority. Equally important is understanding the scale at which functional connectivity occurs among macroalgal and other tropical reef habitats, which will require study of the distances, pathways and vectors of macroalgal biomass movement and utilisation across the seascape (Olds et al., 2018). In doing so, we can then understand how tropical macroalgae contribute to the abundance and productivity of tropical marine ecosystems that comprise a mosaic of connected habitats. This integrated view of ecosystem functions that connect multiple habitat types (coral or otherwise) will be critical in setting appropriate targets for the spatial conservation and management of diverse tropical seascapes.

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AUTHOR'S CONTRIBUTIONS

C.J.F. and S.K.W. conceived the ideas and led the writing of the manuscript; all authors contributed data to the meta-analysis, which C.J.F. collated and analysed; and all authors contributed critically to the writing of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Our meta-analyses are based on a range of independent studies as indicated in the Supporting Information.

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SUPPORTING INFORMATION

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