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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Loss of predation risk from apex predators can exacerbate marine tropicalization caused by extreme climatic events

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Abstract

- Extreme climatic events (ECEs) and predator removal represent some of the most widespread stressors to ecosystems. Though species interactions can alter ecological effects of climate change (and vice versa), it is less understood whether, when and how predator removal can interact with ECEs to exacerbate their effects. Understanding the circumstances under which such interactions might occur is critical because predator loss is widespread and ECEs can generate rapid phase shifts in ecosystems which can ultimately lead to tropicalization.
- 2. Our goal was to determine whether loss of predation risk may be an important mechanism governing ecosystem responses to extreme events, and whether the effects of such events, such as tropicalization, can occur even when species range shifts do not. Specifically, our goal was to experimentally simulate the loss of an apex predator, the tiger shark *Galeocerdo cuvier* effects on a recently damaged seagrass ecosystem of Shark Bay, Australia by applying documented changes to risk-sensitive grazing of dugong *Dugong dugon* herbivores.
- 3. Using a 16-month-field experiment established in recently disturbed seagrass meadows, we used previous estimates of risk-sensitive dugong foraging behaviour to simulate altered risk-sensitive foraging densities and strategies of dugongs consistent with apex predator loss, and tracked seagrass responses to the simulated grazing.
- 4. Grazing treatments targeted and removed tropical seagrasses, which declined. However, like in other mixed-bed habitats where dugongs forage, treatments also incidentally accelerated temperate seagrass losses, revealing that herbivore behavioural changes in response to predator loss can exacerbate ECE and promote tropicalization, even without range expansions or introductions of novel species.
- 5. Our results suggest that changes to herbivore behaviours triggered by loss of predation risk can undermine ecological resilience to ECEs, particularly where longlived herbivores are abundant. By implication, ongoing losses of apex predators may combine with increasingly frequent ECEs to amplify climate change impacts across diverse ecosystems and large spatial scales.

KEYWORDS

climate change, marine heatwave, multiple stressors, predator loss, resilience, risk effects, seagrass, tropicalization

1 | INTRODUCTION

Extreme climatic events (ECEs sensu Jentsch et al., 2007) associated with anthropogenic climate change are becoming more frequent and intense (IPCC, 2019; Oliver et al., 2018). These ECEs alter ecosystems globally and can drive rapid ecosystem tropicalization that is difficult to reverse (e.g. Bennett et al., 2015; IPCC, 2019; Wernberg et al., 2013). As a result, the need to assess the ecosystem effects of ECEs is now critical. It is becoming increasingly clear that species interactions can play major roles in mediating the effects of climate change (i.e. as 'biotic multipliers of climate change', Zarnetske et al., 2012), including in marine ecosystems (Vergés et al., 2014) and in response to ECEs (e.g., Bennett et al., 2015). It is vital, therefore, to understand the role of multiple stressors (Mineur et al., 2015) and species interactions (Zarnetske et al., 2012) in mediating ecological responses to both gradual climate change and ECEs.

Apex predators may be particularly important biotic multipliers of climate change because they interact with many species, have low functional redundancy and are disproportionately vulnerable to exploitation (Heithaus et al., 2008; Ritchie & Johnson, 2009; Zarnetske et al., 2012). Indeed, though not universal, trophic cascades induced by the loss of top predators have been widely documented in terrestrial, aquatic and marine ecosystems (e.g. Estes et al., 2011; Heithaus et al., 2008; Ripple et al., 2014). Disruption of these top-down effects can alter ecosystem function and services (e.g. Atwood et al., 2015; Estes et al., 2011) as well as risk of climate-driven phase shifts (Ling et al., 2009). Maintenance of trophic cascades, particularly those that suppress herbivores, may therefore be crucial to promoting ecosystem recovery and resilience following large climatic disturbances by moderating the effects of consumers which can inhibit ecosystem recovery (e.g. Bennett et al., 2015). This, in some cases, may slow tropicalization.

Like climate change effects, human-driven loss of apex predators is widespread globally (e.g. Estes et al., 2011; Ferretti et al., 2010; Ripple et al., 2014). There is growing evidence that climate change and predators interact to structure ecosystems (e.g. Kirby & Beaugrand, 2009; Kratina et al., 2012), including evidence that predators can mediate the ecological impacts of climate change and climate variability (e.g. Estes et al., 2011; Harley, 2011; Ling et al., 2009; Ripple et al., 2014; Wilmers & Getz, 2005; Wilmers et al., 2006). However, despite widespread co-occurrence of marine predator losses and climate-related disturbances (Halpern et al., 2008), the potential for these stressors to interact remains poorly studied, especially in the field (Crain et al., 2008). If predator loss can exacerbate the ecological impacts of ECEs, apex predator conservation may be an effective strategy to impart resilience from ECEs (sensu Unsworth et al., 2015) by facilitating disturbance recovery until the drivers of climate change can be addressed directly.

One of many ways in which climate change is altering ecosystems is through widespread 'tropicalization', whereby species assemblages in a location shift to resemble those in warmer, more equatorial climates (Vergés et al., 2014). Tropicalization can be driven not only by abiotic forcing brought about by climate change, but also by changes to biotic interactions such as when tropical herbivores expand their ranges into formerly temperate ecosystems and generate novel species interactions (e.g. Bennett et al., 2015; Vergés et al., 2014). These novel biotic interactions can act as biotic multipliers of climate change, altering not only the likelihood of tropicalization, but also how easy or difficult it is to reverse (e.g. Bennett et al., 2015). In addition to gradual warming, recent work has shown that ECEs, particularly marine heatwaves, can drive rapid tropicalization of marine ecosystems (Bennett et al., 2015; Wernberg et al., 2013), and there is some evidence that predator loss can exacerbate phase shifts driven by climate-driven range expansion of herbivores (e.g. Ling et al., 2009). However, it is unclear whether predator loss interacts with the effects of ECEs themselves, particularly in the absence of species range expansions, the most commonly reported driver of biotic tropicalization.

Seagrass meadows provide diverse ecosystem functions (Nordlund et al., 2016 and references therein), including hosting megaherbivores like sea turtles and sirenians that can exert considerable control over seagrass community structure (Jackson, 2001; Nowicki et al., 2018). Despite their importance, seagrass habitats are rapidly disappearing globally because of a variety of stressors, including ECEs (e.g. Fraser et al., 2014; IPCC, 2019; Thomson et al., 2015; Waycott et al., 2009). Seagrass habitats that have large herbivores and are impacted by ECEs therefore represent a valuable chance to determine whether and how changes to top-down control alter ecosystem responses to extreme climate events.

With its abundant populations of both megaherbivores and large tiger sharks, the subtropical seagrass ecosystem of Shark Bay, Western Australia has been a model system in which to study top-down control in the marine environment for more than two decades (Heithaus et al., 2012). The well-studied species interactions in Shark Bay, combined with massive seagrass loss following the most extreme marine heatwave on Western Australian record in 2011 (Fraser et al., 2014; Hobday et al., 2018; Thomson et al., 2015), offer a unique opportunity to assess whether the loss of apex predators can exacerbate the effects of an ECE and promote tropicalization of this subtropical system.

1.1 | Site description and background

Shark Bay (25°45′S, 113°44′E) is a shallow (<15 m), 13,000 km² semi-enclosed subtropical embayment approximately 800 km north of Perth, Western Australia. The bay's seagrass community contains

12 tropical and temperate species but is overwhelmingly dominated (3,700 km² of 4,000 km²) by temperate seagrass Amphibolis antarctica, which is at the tropical limit of its range in Shark Bay (Walker et al., 1988). Amphibolis antarctica is a long-lived ecosystem engineer (sensu Jones et al., 1994) with critical and often irreplaceable ecosystem functions; specifically, A. antarctica greatly increases structural complexity and habitat in the bay through its dense meadows which can be more than 100 cm thick (Walker, 1985), provides food to fauna through primary production and the creation of substrate for epiphytes (Smit et al., 2005) and stabilizes sediment with thick, interlocking rhizome mats (Borowitzka et al., 2006; Burkholder et al., 2013; Smit et al., 2005Walker, 1985; Walker et al., 1988). The most common tropical seagrass in the bay is the much smaller Halodule uninervis (Burkholder, Fourgurean, et al., 2013). While H. uninervis is preferred forage for many herbivores, its biomass, rhizome bed and bed complexity are orders of magnitude lower than that of Amphibolis antarctica, even where both are abundant.

In the Austral summer of 2011, strong La Niña conditions strengthened the Leeuwin Current, increasing the transport of tropical water along the Western Australia coast (Pearce & Feng, 2013) and generating an extreme, category IV marine heatwave (sensu Hobday et al., 2018) known as the 'Ningaloo Niño' (Feng et al., 2013; Pearce & Feng, 2013). This extreme marine heatwave increased water temperatures along Western Australia by 2-5°C for 2 months (Feng et al., 2013; Hobday et al., 2018; Pearce & Feng, 2013), including in Shark Bay (Nowicki et al., 2017). This resulted in catastrophic (>90%) loss of temperate Amphibolis antarctica within the study area (Fraser et al., 2014; Thomson et al., 2015) and opened canopy and substrate to establishment and expansion of the early successional tropical seagrass Halodule uninervis (Nowicki et al., 2017), creating mixed species beds that had been historically rare in the study system (Figures 1 and 2). At larger bay-wide scales, this event triggers the largest known acute loss of dense seagrass (>1,300 km²), though severity of loss was spatially heterogeneous (Strydom et al., 2020). Local water temperature measurements were otherwise relatively normal within the study system, though temperature was elevated by 2.3°C above average in February 2014 (Nowicki et al., 2017).

In other seagrass ecosystems, such mixed species beds are vulnerable to phase shifts driven by dugong and green turtle grazing (Kelkar et al., 2013; Preen, 1995). Dugongs in particular can alter seagrass community composition through destructive excavation foraging, which usually targets tropical seagrasses but can destroy nearby, less disturbance tolerant climax seagrasses incidentally (Masini et al., 2001; Preen, 1995; Wirsing et al., 2007a). This form of top-down control is not thought to be normally dominant in temperate/tropical mixed seagrass beds of Shark Bay for two reasons: first, A. *antarctica*, which is itself not a preferred food source or target of excavation grazing (Burkholder et al., 2012; Wirsing et al., 2007a), establishes dense canopies that limit excavation grazers' access to tropical seagrasses. This makes it difficult for dugongs to find sufficient tropical seagrasses to excavate in full A. *antarctica* meadows (Figure 2a,c). Second, excavation grazing is a dangerous foraging tactic that dugongs rarely



FIGURE 2 Conceptual diagram of the role of trophic cascades and physical feedbacks in determining the stability and structure of *Amphibolis antarctica* beds in Shark Bay. (a) Intact shark populations with normal temperature regimes. (b) Shark populations depleted, but normal temperature regimes keep *A. antarctica* canopy thick and keep dugongs from accessing and excavating tropical seagrasses. (c) An extreme climate event causes *A. antarctica* canopy loss, making tropical seagrasses accessible, but predation risk from abundant tiger sharks keeps excavation by dugongs to a minimum, allowing for stabilization. (d) In a hypothetical scenario where tiger sharks (and the predation risk they generate) were removed, extreme-driven canopy loss is exacerbated by dugong excavation foraging. (a) and (b) have been documented elsewhere (see Heithaus et al., 2012); this study tests scenarios (c) and (d). Photographs: SBERP



FIGURE 1 Representative states of the study area's *Amphibolis antarctica* beds before and after the 2011 marine heatwave. Notice abundance of tropical early successional seagrass *Halodule uninervis* (right panel, small shoots with white arrow) growing in between the larger shoots of *Amphibolis antarctica*. Photograph credit: J. Thomson, R. Nowicki

undertake in Shark Bay because of predation risk from tiger sharks *Galeocerdo cuvier*, which are abundant and play an important role in shaping seagrass ecosystem structure and function in Shark Bay (Burkholder et al., 2013; Heithaus et al., 2012; Wirsing et al., 2007a, 2007b, 2007c; Figure 2a,b). However, ECE-mediated loss of A. *antarctica* has made sparse seagrass beds more common (Bayliss et al., 2019) and has promoted the expansion, density and accessibility of tropical seagrasses to excavators (Nowicki et al., 2017), increasing the potential for excavation grazing to reinforce tropicalization by exacerbating a phase shift to a tropical seagrass community (Figure 2c). If apex predators (in this case, tiger sharks) were extirpated and predation risk was lowered, as occurs in ecosystems globally (Estes et al., 2011; Ferretti et al., 2010; Ripple et al., 2014), then the ensuing combination could result in a permanent tropicalization, typified by a low biomass or even seagrass depauperate state (Figure 2d).

We used this 2011 ECE as a natural experiment to experimentally simulate changes in dugong foraging behaviour consistent with tiger shark extirpation. In doing so, we sought to determine whether a combination of simulated predator loss and climatic disturbance could destabilize remaining A. antarctica beds and reinforce a phase shift towards tropicalization of the seagrass community. More generally, our aim was to evaluate whether predation risk from apex predators can act as a resilience mechanism for ecosystems that include large herbivores and suffer a large disturbance to their primary producer communities. To determine this, we performed a 16-month-field experiment in which divers applied risk-sensitive foraging tactics to disturbed seagrass beds at rates consistent with complete tiger shark extirpation and loss of predation risk to Shark Bay's dominant megaherbivore, the dugong Dugong dugon. Our specific goals were to determine a priori (a) if emulated tiger shark Galeocerdo cuvier removal would drive habitat tropicalization by reducing A. antarctica cover through incidental removal during dugong excavation while allowing H. uninervis to proliferate, and post hoc (b) whether such effects are dependent on the strength of initial seagrass loss.

2 | MATERIALS AND METHODS

2.1 | Site establishment

In April-May 2013, 30 experimental plots, each measuring 3 m \times 3 m, were placed at 2-3 m depth in the interiors of two

seagrass banks located 7-8 km ENE of Monkey Mia in Shark Bay's Eastern Gulf (Figure 3). This series of banks has been the subject of over two decades of work investigating the role that predatorprey dynamics play in structuring marine benthic ecosystems (Heithaus et al., 2012). Shark Bay is a hypersaline environment, and salinity in the study area averages 45 ppt (Walker, 1985). Each plot was placed in a degraded A. antarctica bed that was characterized by reduced A. antarctica cover (10%-60%), prevalence of exposed, dying A. antarctica rhizome tissue, presence of the early successional tropical seagrass H. uninervis and generally low macroalgae cover (Figure 1, third panel). Plots were placed in a blocked design on two banks; 18 plots were placed on a heavily impacted bank (mean initial A. antarctica cover = 17.3%, SD = 5.2%), and 12 on a moderately impacted bank (mean initial A. antarctica cover = 33.1%, SD = 11.3%, Figure 3) to represent the heterogeneity of seagrass loss. For reference, healthy A. antarctica beds typically approach or meet 100% cover. Each treatment level (control, moderate herbivory, intense herbivory) was equally represented within each block, and plots near each other were grouped into trios of similar initial seagrass cover before being randomly assigned a treatment. Plots were marked with a post at each corner and were generally farther than 2 m from each other. The mean H. uninervis cover was similar on both banks (mean 46.7%, SD = 21.4%, Welch's t test: $t_{24.2}$ = 0.09, p = 0.93). Macroalgae cover was slightly higher on the heavily impacted bank (median of 5.8% vs. 2.4%, Mann-Whitney test, W = 118, p = 0.0015) but was generally very low (mean = 4.8%, median 3.8%, SD = 3.8%).

2.2 | Estimation of dugong foraging rates

Because experimental manipulation of tiger shark predation risk is not feasible, we simulated dugong foraging impacts manually. To determine appropriate foraging rates, we used published data on predation risk-sensitive foraging by dugongs in the study area (Wirsing et al., 2007a, 2007b, 2007c) to estimate the magnitude of changes to dugong habitat, foraging and thus foraging density/pressure that should occur in high-risk shallow seagrass bank habitats if tiger sharks were extirpated and these habitats became low risk (see Heithaus et al., 2012 for an overview).

Dugong foraging effort, expressed in number of seconds of foraging effort per plot per month (λ), was calculated by scaling down

FIGURE 3 Location of experiment in relation to Shark Bay generally (asterisk) (a) and within the long-term study area specifically (b). Tan denotes land, blue denotes deep water (4–15 m) and green denotes shallow banks (<4 m depth). Banks were historically heavily covered in seagrass, though cover is now greatly reduced within the study area



bank-scale estimates of foraging dugong density calculated for this system (Wirsing et al., 2007b) to the scale of individual plots. Dugong abundances and activity levels vary seasonally and with changes to water temperature and shark abundance (Wirsing et al., 2007b), so λ was calculated monthly to reflect larger regional scale seasonal shifts in dugong abundance. Focal follows of dugongs in the study area suggest that trails are excavated at the rate of *c*. 10 cm of horizontal progress $\times \sec^{-1}$ (Nowicki, pers. obs.; Wirsing et al., 2007a), so λ was divided by 10 to determine the number of 1-m feeding trails applied per plot for each month (rounded to nearest integer). A 15 cm \times 100 cm rebar grazing frame was used to ensure a constant area and shape of grazing treatments.

Dugongs can forage via two tactics: shoot cropping and rhizome excavation (Wirsing et al., 2007a). Because excavation foraging is more profitable to dugongs than cropping the tops of shoots (Anderson, 1982, 1998; Wirsing et al., 2007a), we simulated excavation as long as dense stands of tropical seagrass were present in the plot (i.e. if at least three of five panels of grazing frame contained *H. uninervis*). We always targeted the densest stands of *H. uninervis* and avoided *A. antarctica* if possible, both to mimic the most adaptive dugong grazing behaviour, and to ensure any rates of incidental *A. antarctica* removal were conservative. When *A. antarctica* was present in the excavation frame, however, it was removed to mimic the incidental removal of non-target seagrasses that occur during excavation foraging, which can have critical impacts to mixed species seagrass beds (Preen, 1995).

Excavation trails measured 15 cm W × 100 cm L × 4 cm D and were created with hand trowels to generate feeding scars consistent with dugong excavation foraging. Excavation removed all aboveground and below-ground biomass within the scar depth, similar to actual dugong excavation trails (De longh et al., 1995; Masini et al., 2001; Nakaoka et al., 2002; Preen, 1995). Seagrass recovery from artificial dugong excavation trails is not significantly different from natural feeding trails (De longh et al., 1995; Nakaoka & Aioi, 1999), so we are confident our treatments accurately reflected natural dugong excavation. In very rare (<5%) cases where sufficient *H. uninervis* was sparse, an equal area was grazed by cropping *A. antarctica* shoots with a knife where the leaf bundle meets the stem to mimic the dugong 'cropping' feeding strategy.

2.3 | Data collection and application of grazing treatments

Our experiment included three treatment levels: control, moderate herbivory and intense herbivory. Grazing treatments were applied every 30–60 days from May 2013 to August 2014. Control plots were visited to collect data but did not undergo simulated grazing to reflect the current, high-risk landscape of Shark Bay, because tiger shark abundance did not change following the ECE (Nowicki et al., 2019). The moderate herbivory treatment (λ grazing per visit) simulated the grazing effort that would be expected if dugong abundance remained constant but dugong habitat use shifted entirely towards shallow seagrass banks where the experiment was established, as would be expected if predation risk was eliminated (Wirsing et al., 2007c). These shallow seagrass beds yield both the highest food availability and highest risk of tiger shark predation for dugongs (Wirsing et al., 2007b). Intense grazing treatments (1.5λ grazing per visit) acted as an upper bound for potential herbivore effects and to emulate both a behavioural and numerical response of dugong populations to shark loss. Multiple lines of evidence suggest the dugong densities upon which λ is based are robust (see Section 4).

At 0, 7, 12 and 16 months into the experiment, we estimated cover of A. *antarctica*, H. *uninervis* and macroalgae species in each plot using a 60 cm \times 60 cm quadrat placed 25 times in a 5 \times 5 grid pattern within the plot. These cover estimates were then averaged. Plots that were destroyed from sudden widespread seagrass defoliation or storm action were excluded from analysis from that time point forward as studying effects of storm blowouts were outside the scope of this experiment.

2.4 | Statistical analyses

We applied mixed effects models and model selection using the GLMMTMB package (Brooks et al., 2017) in RStudio version 1.2.1335 (RStudio Team, 2019) to determine the influences of grazing treatment, time since start, bank and their interactions on cover estimates of *A. antarctica*, *H. uninervis* and macroalgae. Five individual a priori models were run for each macrophyte group (Table 1). In each, plot ID was retained as a random effect to account for repeated measures. Percent cover data were converted to proportion data, and models were run using the beta distribution (Zeileis et al., 2010).

Data were analysed using a model selection approach (Anderson, 2007; Anderson & Burnham, 2004). Specifically, we applied multimodel inference and model averaging to evaluate whether parameters

TABLE 1 Models applied to macrophyte data, along with the
hypotheses they support if the model performs well relative to
other models. Month since start (Month), bank identity (Bank), and
grazing treatment (Treat) were fixed effects. Plot ID was included
as a random effect to account for temporal autocorrelation of
the repeated measures. Asterisks indicate main effects and their
interactions; colons indicate interaction effects only

Model	Fixed effects	Hypothesis
1	Month	Seagrass cover changes over time only
2	$Month \times Bank$	Cover change differs by bank only
3	Month × Treat	Cover change differs by treatment only
4	Month + Bank + Treat + Month: Treat + Month:Bank	Cover change differs by bank and treatment, but the effects of treatment do not differ by bank
5	$Month \times Bank \times Treat$	Cover change differs by bank and treatment, and the effect of treatment differs by bank

significantly contributed to model fit (Anderson, 2007; Anderson & Burnham, 2004). Model selection, model averaging and multi-model inference differ from traditional frequentist statistics that rely on *p*values (which are problematic in their binary treatment of 'significant' and 'non-significant', Halsey, 2019; Hurlbert et al., 2019). Instead, this increasingly popular information-theoretic approach to inference compares competing models which represent 'multiple working

TABLE 2 Initial cover and absolute and relative changes in percent cover of *Amphibolis antarctica*, *Halodule uninervis* and benthic macroalgae over the course of the experiment. *SE* = standard error

	Initial cover	SE	Final cover	SE	% relative change
Amphibolis antarctica					
Control (all banks)	21.2%	4.3%	16.3%	4.8%	-23.1%
Standard (all banks)	24.5%	3.5%	17.3%	4.9%	-29.4%
Intense (all banks)	23.9%	3.2%	12.4%	3.0%	-48.1%
Halodule uninervis					
Control (all banks)	45.6%	7.0%	35.4%	7.7%	-22.4%
Standard (all banks)	42.2%	5.4%	23.3%	6.0%	-44.8%
Intense (all banks)	52.2%	8.3%	14.4%	1.7%	-72.4%
Macroalgae					
Control (all banks)	5.5%	2.1%	2.5%	1.2%	-54.5%
Standard (all banks)	4.8%	1.1%	2.9%	0.9%	-39.6%
Intense (all banks)	4.2%	0.9%	2.5%	0.5%	-40.5%

hypotheses' (Chamberlin, 1890) using Akaike's information criterion, or AIC (Anderson, 2007), and allows for information to be integrated between competing models to make inferences with gradients of evidence rather than a hard threshold (model averaging). This approach is particularly useful when several models perform similarly well and is useful because it recognizes that even suboptimal models may include valuable information about parameters (in this case, month since start, treatment and bank).

3 | RESULTS

Of the 30 plots established, 29 remained intact for at least 12 months and were retained for analysis; 23 remained intact until the experiment's end. Destroyed plots were compromised mostly by smallscale physical erosion (blowout) events, and were evenly distributed between treatments (two each in control and intense grazing treatments, three in moderate treatments). All plot losses occurred exclusively on the moderately impacted eastern bank.

Macrophyte cover declined for all species in all treatments, though the level of decline varied with treatment level. Cover of *H. uninervis* declined fastest under intense simulated herbivory (from 52.2% to 14.4% over 16 months), followed by moderate herbivory (42.4% to 23.3%) and slowest under control conditions (45.6% to 35.4%, Table 2, Figure 4). Interestingly, A. *antarctica* displayed the same patterns despite not being targeted by grazing; cover declined from 23.9% to 12.4% in intense grazing treatments, 24.5% to 17.3% in moderate grazing treatments, and 21.2% to 16.3% in control



FIGURE 4 Effect of herbivory treatment on cover over time for *Amphibolis antarctica, Halodule uninervis* generally (black squares and lines, bars = $\pm SE$) and by bank (red and blue squares and dotted lines). Scale bars are the same across all plots. Square diameter correlates directly with number of plots in sample. In some cases, error bars are too small to be shown

TABLE 3 Results of model construction and multi-model inference for each macrophyte group. M = month, B = bank, T = treatment. An interaction of treatment and month (i.e. T:M; bold) indicates an effect of treatment on percent cover over time. Cumulative weight of all a priori models is included to the right, while below are combined weights of all models including that parameter across the five a priori models (i.e. the total weight of each model divided by the cumulative weight of all a priori models)

	Model parameters							Log			Cumulative
Species	М	В	т	B:M	T:M	B:T:M	df	likelihood	∆AlCc	Weight	weight
Amphibolis	х	х		х			6	171.863	0	35.4%	35.4%
Amphibolis	х	х	х	х	х	х	12	178.948	0.2	31.5%	66.9%
Amphibolis	х	х	х	х	х		10	176.348	0.4	28.4%	95.3%
Amphibolis	х						4	140.929	57.4	0.0%	95.3%
Amphibolis	х		х		х		8	143.79	60.8	0.0%	95.3%
Total weights	100.0%	100.0%	62.9%	100.0%	62.9%	33.2%					
Halodule	х		х		х		8	61.586	0	44.0%	44.0%
Halodule	х						4	56.049	2	16.0%	60.0%
Halodule	х	х	х	х	х	х	12	65.014	2.93	10.1%	70.1%
Halodule	х	х	х	х	х		10	61.773	4.42	4.8%	74.9%
Halodule	х	х		х			6	56.118	6.32	1.9%	76.8%
Total weights	100.0%	21.9%	76.7%	21.9%	76.7%	13.2%					
Macroalgae	х	х		х			6	245.173	0	78.0%	78.0%
Macroalgae	х	х	х	х	х		10	246.424	7	2.4%	80.4%
Macroalgae	х	х	х	х	х	х	12	248.89	7.13	2.2%	82.6%
Macroalgae	х						4	235.629	14.6	0.1%	82.7%
Macroalgae	х		x		х		8	236.37	22.3	0.0%	82.7%
Total weights	100.0%	99.9%	5.6%	99.9%	5.6%	2.7%					

treatments (Table 2, Figure 4). Macroalgae cover remained low and displayed no sensitivity to grazing treatment (Table 2, Figure 4).

The suite of a priori models performed well as measured by cumulative Akaike weights (Table 3). Indeed, out of all possible model iterations, the a priori model suite for A. antarctica accounted for 95% of model weight (i.e. all other possible models only received 5% of weights when combined), whereas the H. uninervis and macroalgae model suites received 77% and 83% of all model weights respectively (Table 3). Among the five a priori models for H. uninervis, an interaction of month and treatment received high support with 76.7% of total weights, suggesting a real treatment effect of simulated herbivory on H. uninervis cover over time. Similarly, most of the weight (62.9%) in the A. antarctica model suite went to models that included an interaction of month and treatment (Table 3). Interestingly, though only one of five models included an interaction of month, bank and treatment (indicating that treatment effects differ by bank), this model was assigned a disproportionately large amount of weight (33.2%) given to the A. antarctica model suite, suggesting that treatment effects on A. antarctica may differ by bank or initial A. antarctica cover (which differed by bank). Indeed, whereas general seagrass recovery did not occur over the course of the experiment, A. antarctica cover remained stable in control and moderate grazing treatments on the moderately impacted eastern bank where initial cover was higher (Figure 4). Month and bank were both extremely strong predictors of A. antarctica cover, being represented in 100% of model weights. Month was similarly important for

H. uninervis but bank alone was less important, representing 21.9% of model weights. Models including a treatment:month interaction on macroalgae received little support, with 5.6% of model weights (Table 3). Generally, herbivory treatments resulted in declines of both tropical *H. uninervis* and the temperate *A. antarctica*, even though treatments overwhelming targeted *H. uninervis* (Figure 4, Table 2).

4 | DISCUSSION

Our results suggest: (a) predator loss can reduce resilience to extreme climatic events through reducing predation risk to herbivores and inhibiting recovery from disturbance (treatment effect); (b) this effect may be mediated by the intensity of initial disturbance or quantity of plant cover remaining (treatment:bank interaction); and (c) in transition zones (like subtropical ecosystems), this may result in behaviourally mediated tropicalization without range expansions of producers or consumers. By implication, apex predator loss may in some cases be an important mechanism in governing the resilience of ecosystems to ECEs by facilitating recovery, one of the components of resilience (sensu Unsworth et al., 2015). Indeed, widespread co-occurrence of predator loss and climate change may provide many opportunities for these two stressors to interact to exacerbate the impact of climate extremes and to drive tropicalization.

4.1 | Impact to climax seagrass

Amphibolis antarctica cover declined generally, but this species' decline was accelerated under herbivory treatments even though it was not being targeted by these treatments (Figure 4). With the exception of anomalously high temperatures (2.3°C) in February 2014, the temperature regime in the study area was similar to longterm averages over the experimental duration (Nowicki et al., 2017), suggesting that subsequent heatwaves play at most a minor role in the continued seagrass loss. Importantly, declines in the control and moderate herbivory treatments were driven mostly by declines in the already heavily impacted western bank (Figure 4), suggesting that these beds are likely more vulnerable not only to top-down control, but also to general collapse. This also suggests that the strength of top-down control may be influenced by initial post-disturbance seagrass cover. Indeed, the A. antarctica beds most heavily affected by the initial disturbance continued to break up over the course of this experiment across the study system (Nowicki et al., 2017), which would explain the loss of A. antarctica in those control plots. Unfortunately, we cannot unequivocally attribute this potential interaction between treatment effect and bank to initial seagrass density alone. Nonetheless, these results suggest that the vulnerability of plant communities to post-disturbance herbivory (and therefore predator loss) likely interact with disturbance severity. This has implications for the spatial component of seagrass recovery, since seagrass loss was spatially heterogeneous (Strydom et al., 2020).

Amphibolis antarctica is a late successional seagrass species with recovery rates that span years to decades following large losses, and recovery of dense seagrass habitats has been slow both in the study area and in Shark Bay generally (Bayliss et al., 2019; Nowicki et al., 2017). The pace of A. antarctica decline in our treatments (i.e. 30%-50% relative losses over 16 months) implies that loss of tiger shark predation risk could quickly drive reinforce tropicalization towards a structurally simplified tropical seagrass community. The capability for dugong excavation to generate such shifts has been demonstrated elsewhere (e.g. Aragones & Marsh, 1999; Preen, 1995). The mechanism for such decline hinges on the establishment of mixed species plant assemblages that differ in disturbance tolerance, as well as destructive herbivore feeding methods (i.e. incidental destruction during foraging). As such, recovery of A. antarctica via seedling establishment may result in a high rate of recruitment failure if such seedlings establish in tropical or mixed seagrass beds, further inhibiting recovery in the absence of predation risk.

4.2 | Impact to pioneer seagrass and benthic macroalgae

Whereas macroalgae do not play a dominant role in the postdisturbance macrophyte community of Shark Bay, tropical seagrasses are becoming more common across the study system since the heatwave (Nowicki et al., 2017). Herbivory treatments had strong effects on H. uninervis cover (Figure 4), but this is unlikely to facilitate A. antarctica recovery for several reasons. First, H. uninervis is a disturbance tolerant seagrass with a dormant seed bank and fast expansion rates (Larkum et al., 2007) that can recolonize rapidly following grazing (weeks to months, Preen, 1995, Nakaoka & Aioi, 1999, Aragones & Marsh, 1999, also see dynamics in Figure 4). Second, many herbivores (including dugongs) revisit sites to feed after vegetation recolonization occurs (e.g. Bjorndal, 1980; De longh et al., 2007; Preen, 1995), which would spur additional incidental loss of A. antarctica. Finally, H. uninervis declined in all plots, including control plots, despite expanding systemwide (Nowicki et al., 2017), suggesting that declines were at least partially driven by patch migration (Walker et al., 2007) out of plots. Indeed, plots were established non-randomly in areas of initially high H. uninervis cover, and a prior herbivore exclosure experiment performed near our own noted high variability in H. uninervis shoot densities within plots over 600 days (Burkholder, Heithaus, et al., 2013). Importantly, patch migration may actually accelerate dugong-mediated loss of remaining sparse A. antarctica if H. uninervis migrates through damaged A. antarctica beds and attracts dugong excavation grazing to them. Thus, early successional seagrasses are likely to persist and continue to attract destructive excavation grazing to degraded beds of A. antarctica.

Because we used a naturally occuring extreme event opportunistically to perform our experiment, estimates of predation risk and dugong density had to be parameterized with pre-heatwave data. Fortunately, six lines of evidence suggest that the fundamental mechanisms responsible for the pre-decline behaviourally mediated trophic cascade that typifies the study system (Heithaus et al., 2012) remain robust. First, the abundance of tiger sharks and the risk-sensitive habitat use patterns of remaining dugongs remain the same as before 2011 (Nowicki et al., 2019), indicating predation risk remains an important structuring mechanism to enhance postdisturbance stability of A. antarctica beds. Second, while dugong abundances declined by two thirds in the study system between the pre-disturbance period and 2014 (Nowicki et al., 2019), this trend the product of temporary emigration and reduced calf fecundity immediately after the event, rather than mass mortality, and is therefore fairly quickly reversible. Indeed, mass dugong mortality results in widespread dugong strandings (e.g. Great Barrier Reef Marine Park Authority, 2014; Preen & Marsh, 1995), neither of which were observed nor reported in Shark Bay, including by fisheries staff and wildlife tour operators that spend hundreds to thousands of hours per year navigating the bay (B. Francis of Department of Primary Industries and Regional Development [DPIRD], and Monkey Mia Wildsights [MMW], pers. comm. Oct 2019). Instead, a lack of dugong calves were reported following the heatwave both from operators on the water and from aerial surveys (Bayliss et al., 2019; DPIRD and MMW pers. comm. Oct. 2019), indicating that population-level effects were likely most caused by emigration and reproductive failure. Indeed, dugongs regularly move hundreds of kilometres and immigrate to alternative foraging locations following seagrass loss, including between Shark Bay and Ningaloo Reef several hundred kilometres

to the North (Gales et al., 2004; Hodgson, 2007; Holley et al., 2006; Sheppard et al., 2006). Third, dugongs retain a spatial memory of productive seagrass habitat and return to disturbed habitats once tropical seagrasses recover (Gales et al., 2004; Hodgson, 2007; Holley et al., 2006; Marsh & Lawler, 2001; Preen & Marsh, 1995; Sheppard et al., 2006). Such recovery has been underway in Shark Bay since 2014 (Bayliss et al., 2019; Kendrick et al., 2019; Nowicki et al., 2017) and both fisheries officers and wildlife tour operators have reported returns to pre-heatwave dugong densities since 2016 (DPIRD and MMW, pers. comm. Oct. 2019). Fourth, aerial surveys undertaken in 2018 indicate that dugong densities within Shark Bay are once again similar to pre-heatwave levels both in Shark Bay and Ningaloo reef (Bayliss et al., 2019), even though A. antarctica recovery has not kept pace. Fifth, the strongest predictor of dugong abundance from the 2018 surveys was the presence of sparse seagrass beds (Bayliss et al., 2019), which are the exact habitats of relevance to the present study. All of this evidence supports our inferences that dugong population recovery has occurred before A. antarctica recovery and that the density estimates used in this experiment are robust. Finally, dugongs can exert strong top-down control quickly upon their return, denuding even dense seagrass beds in a matter of weeks (e.g. Masini et al., 2001; Preen, 1995). Because A. antarctica will take years to decades to recover (Bayliss et al., 2019; Kendrick et al., 2019; Nowicki et al., 2017), we are confident that our results are relevant to Shark Bay's current state, and that predation risk is likely to remain a relevant driving mechanism in the recovery or tropicalization of this system.

4.3 | Implications for the loss of resilience and tropicalization

Extreme climatic events can cause dramatic and abrupt changes to ecosystems, including tropicalization (e.g. Vergés et al., 2014; Wernberg et al., 2013). Most studies of marine tropicalization, however, have focused either partially or entirely on range expansions of primary producers or consumers, which can generate novel species interactions (e.g. Bennett et al., 2015; Heck et al., 2015; Hyndes et al., 2016; Ling et al., 2009; Pecl et al., 2017; Vergés et al., 2014; Zarco-Perello et al., 2017). This is also true among studies that focus on the role of predator-prey interactions in tropicalization (e.g. Ling et al., 2009, but see Bonaviri et al., 2017). Here, we show evidence that climate change can promote tropicalization without range expansions of novel species. Instead, the tropicalization of Shark Bay would be amplified by a combination of loss of predation risk and differential climate vulnerability of already co-occurring foundation species (i.e. response diversity). Such conditions would be expected in areas where biome ranges overlap (e.g. subtropical ecosystems), and where predator populations have been reduced. This mechanism of tropicalization should be explored elsewhere and incorporated into a more general framework to predict ecosystem responses to ECEs, and how predator loss may mediate those responses.

Whereas predator loss and climate change are both global threats to the functional integrity and resilience of ecosystems, the temporal and spatial scales at which these two stressors can be functionally addressed differ greatly. Management at local and regional levels for ecological resilience may be key to preventing catastrophic phase shifts and tropicalization while long-term action is taken on climate change (e.g. DeYoung et al., 2008). Conservation and restoration of top predators and the ecological resilience they can impart may be a critical (if ambitious) short-term strategy to reduce the impacts of ECEs as governments move to address climate change directly. Though it remains unclear how widely predation risk may grant such resilience, the widespread co-occurrence of apex predator loss and climate change suggests broad potential for interaction. More work is needed to determine the ecological conditions under which predator restoration is most likely to yield measurable increases in resilience to ECEs generally. This strategy of climate resilience through predator restoration is likely to be most effective in systems with highly iteroparous herbivores (such as Shark Bay), which are likely to invest highly in anti-predator behaviour (Clark, 1994) and thus propagate behaviourally mediated trophic cascades. Indeed, such a strategy for local resilience to climate extremes may become increasingly important as megafauna restoration efforts such as those for the herbivorous green turtle Chelonia mydas continue to succeed (Heithaus et al., 2014). Without a concomitant effort to also restore the predators of these herbivores, the resilience of communities to future climate disturbances and ensuing tropicalization may be reduced. Identifying the conditions under which predator effects are most likely to yield increased resilience to ECEs and tropicalization will be critical to determining the potential effectiveness of predator restoration as a technique to increase ecological resilience and maintain ecological function in an increasingly extreme world.

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AUTHORS' CONTRIBUTIONS

R.J.N. and M.R.H. designed the study; R.J.N. and J.A.T. performed the research; R.J.N. wrote the manuscript. All the authors provided methods and/or materials, and contributed significantly to manuscript preparation.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/ 10.5061/dryad.59zw3r261 (Nowicki et al., 2021).

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REFERENCES

- Anderson, D. R. (2007). Model based inference in the life sciences: A primer on evidence. Springer Science & Business Media.
- Anderson, P. K. (1982). Studies of dugongs at Shark Bay, Western Australia. II.* Surface and subsurface observations. Wildlife Research, 9, 85–99.
- Anderson, P. K. (1998). Shark Bay dugongs (*Dugong dugon*) in summer.
 II: Foragers in a Halodule-dominated community. *Mammalia*, 62, 409-426.
- Anderson, D., & Burnham, K. (2004). Model selection and multi-model inference (2nd ed., Vol. 63, p. 10). Springer-Verlag.
- Aragones, L., & Marsh, H. (1999). Impact of dugong grazing and turtle cropping on tropical seagrass communities. *Pacific Conservation Biology*, 5, 277–288.
- Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., Fourqurean, J., & Macreadie, P. I. (2015). Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*, *5*, 1038.
- Bayliss, P., Raudino, H., Hutton, M., Murray, K., Waples, K., & Strydom, S. (2019). Modelling the spatial relationship between dugong (Dugong dugon) and their seagrass habitat in Shark Bay Marine Park before and after the marine heatwave of 2010/11. Dugongs & Seagrass NESP Report, 2(2019), 55p.
- Bennett, S., Wernberg, T., Harvey, E. S., Santana-Garcon, J., & Saunders, B. J. (2015). Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, 18, 714–723.
- Bjorndal, K. A. (1980). Nutrition and grazing behavior of the green turtle Chelonia mydas. Marine Biology, 56, 147–154.
- Bonaviri, C., Graham, M., Gianguzza, P., & Shears, N. T. (2017). Warmer temperatures reduce the influence of an important keystone predator. *Journal of Animal Ecology*, 86(3), 490–500.
- Borowitzka, M. A., Lavery, P. S., & Van Keulen, M. (2006). Epiphytes of seagrasses. In A. Larkum, R. Orth, & C. Duarte (Eds.), Seagrasses: Biology, ecology and conservation (pp. 441–461). Springer.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zeroinflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400.
- Burkholder, D. A., Fourqurean, J. W., & Heithaus, M. R. (2013). Spatial pattern in seagrass stoichiometry indicates both N-limited and Plimited regions of an iconic P-limited subtropical bay. *Marine Ecology Progress Series*, 472, 101–115.
- Burkholder, D. A., Heithaus, M. R., & Fourqurean, J. W. (2012). Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem. *Marine & Freshwater Research*, 63, 1051–1058.
- Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A., & Dill, L. M. (2013). Patterns of top-down control in a seagrass ecosystem: Could a roving apex predator induce a behaviour-mediated trophic cascade? *Journal of Animal Ecology*, *82*, 1192–1202.
- Chamberlin, T. C. (1890). The method of multiple working hypotheses. *Science*, 15(366), 92–96.

- Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, 5, 159–170.
- Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- De longh, H. H., Kiswara, W., Kustiawan, W., & Loth, P. E. (2007). A review of research on the interactions between dugongs (Dugong dugon Müller 1776) and intertidal seagrass beds in Indonesia. *Hydrobiologia*, 591(1), 73–83.
- De longh, H. H., Wenno, B. J., & Meelis, E. (1995). Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany*, 50, 1–19.
- Deyoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R. I., Scheffer, M., & Werner, F. (2008). Regime shifts in marine ecosystems: Detection, prediction and management. *Trends in Ecology & Evolution*, 23, 402–409.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306.
- Feng, M., McPhaden, M. J., Xie, S.-P., & Hafner, J. (2013). La Niña forces unprecedented Leeuwin Current warming in 2011. *Scientific Reports*, 3, 1277.
- Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13, 1055–1071.
- Fraser, M. W., Kendrick, G. A., Statton, J., Hovey, R. K., Zavala-Perez, A., & Walker, D. I. (2014). Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. *Journal of Ecology*, 102, 1528–1536. https://doi.org/10.1111/1365-2745.12300
- Gales, N., McCauley, R. D., Lanyon, J., & Holley, D. (2004). Change in abundance of dugongs in Shark Bay, Ningaloo and Exmouth Gulf, Western Australia: Evidence for large-scale migration. Wildlife Research, 31, 283–290. https://doi.org/10.1071/WR02073
- Great Barrier Reef Marine Park Authority. (2014). Great Barrier Reef Outlook Report 2014. GBRMPA.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319, 948–952. https:// doi.org/10.1126/science.1149345
- Halsey, L. G. (2019). The reign of the p-value is over: What alternative analyses could we employ to fill the power vacuum? *Biology Letters*, 15(5), 20190174.
- Harley, C. D. (2011). Climate change, keystone predation, and biodiversity loss. *Science*, 334, 1124–1127. https://doi.org/10.1126/scien ce.1210199
- Heck Jr, K. L., Fodrie, F. J., Madsen, S., Baillie, C. J., & Byron, D. A. (2015). Seagrass consumption by native and a tropically associated fish species: Potential impacts of the tropicalization of the northern Gulf of Mexico. *Marine Ecology Progress Series*, 520, 165–173. https://doi. org/10.3354/meps11104
- Heithaus, M. R., Alcoverro, T., Arthur, R., Burkholder, D. A., Coates, K. A., Christianen, M. J. A., Kelkar, N., Manuel, S. A., Wirsing, A. J., Kenworthy, W. J., & Fourqurean, J. W. (2014). Seagrasses in the age of sea turtle conservation and shark overfishing. *Frontiers in Marine Science*, 1, 28. https://doi.org/10.3389/fmars.2014.00028
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends* in Ecology & Evolution, 23, 202–210. https://doi.org/10.1016/j. tree.2008.01.003
- Heithaus, M. R., Wirsing, A. J., & Dill, L. M. (2012). The ecological importance of intact top-predator populations: A synthesis of 15 years of

research in a seagrass ecosystem. *Marine and Freshwater Research*, 63, 1039–1050. https://doi.org/10.1071/MF12024

- Hobday, A., Oliver, E., Sen Gupta, A., Benthuysen, J., Burrows, M., Donat,
 M., Holbrook, N., Moore, P., Thomsen, M., Wernberg, T., & Smale, D.
 (2018). Categorizing and naming marine heatwaves. *Oceanography*, 31, 162–173. https://doi.org/10.5670/oceanog.2018.205
- Hodgson, A. J. (2007). The distribution, abundance and conservation of dugongs and other marine megafauna in Shark Bay Marine Park, Ningaloo Reef Marine Park and Exmouth Gulf. Report to the Western Australia Department of Environment and Conservation September.
- Holley, D. K., Lawler, I. R., & Gales, N. J. (2006). Summer survey of dugong distribution and abundance in Shark Bay reveals additional key habitat area. Wildlife Research, 33, 243–250. https://doi.org/10.1071/WR05031
- Hurlbert, S. H., Levine, R. A., & Utts, J. (2019). Coup de grâce for a tough old bull: "Statistically significant" expires. *The American Statistician*, 73(sup1), 352–357. https://doi.org/10.1080/00031 305.2018.1543616
- Hyndes, G. A., Heck, K. L., Vergés, A., Harvey, E. S., Kendrick, G. A., Lavery, P. S., McMahon, K., Orth, R. J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S., & Wilson, S. (2016). Accelerating tropicalization and the transformation of temperate seagrass meadows. *BioScience*, 66, 938–948. https://doi.org/10.1093/biosci/biw111
- IPCC. (2019). Summary for policymakers. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. Weyer (Eds.) IPCC special report on the ocean and cryosphere in a changing climate. in press.
- Jackson, J. B. (2001). What was natural in the coastal oceans? Proceedings of the National Academy of Sciences, 98(10), 5411–5418.
- Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. Frontiers in Ecology and the Environment, 5, 365–374.
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69(3), 373–386.
- Kelkar, N., Arthur, R., Marbà, N., & Alcoverro, T. (2013). Greener pastures? High-density feeding aggregations of green turtles precipitate species shifts in seagrass meadows. *Journal of Ecology*, 101, 1158– 1168. https://doi.org/10.1111/1365-2745.12122
- Kendrick, G. A., Nowicki, R. J., Olsen, Y. S., Strydom, S., Fraser, M. W., Sinclair, E. A., Statton, J., Hovey, R. K., Thomson, J. A., Burkholder, D. A., McMahon, K. M., Kilminster, K., Hetzel, Y., Fourqurean, J. W., Heithaus, M. R., & Orth, R. J. (2019). A Systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community. *Frontiers in Marine Science*, *6*, 455. https://doi.org/10.3389/fmars.2019.00455
- Kirby, R. R., & Beaugrand, G. (2009). Trophic amplification of climate warming. Proceedings of the Royal Society B: Biological Sciences, 276, 4095–4103. https://doi.org/10.1098/rspb.2009.1320
- Kratina, P., Greig, H. S., Thompson, P. L., Carvalho-Pereira, T. S. A., & Shurin, J. B. (2012). Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, 93, 1421–1430. https://doi.org/10.1890/11-1595.1
- Larkum, A. W., Orth, R. J., & Duarte, C. (2007). Seagrasses: Biology, ecology and conservation. Springer Science & Business Media.
- Ling, S. D., Johnson, C. R., Frusher, S. D., & Ridgway, K. R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences of the United States of America, 106, 22341–22345. https://doi. org/10.1073/pnas.0907529106
- Marsh, H., & Lawler, I. (2001). Dugong distribution and abundance in the southern Great Barrier Reef Marine Park and Hervey Bay: Results of an aerial survey in October-December 1999. GBRMPA Research Publication, 70.
- Masini, R. J., Anderson, P. K., & McComb, A. J. (2001). A Haloduledominated community in a subtropical embayment: Physical

environment, productivity, biomass, and impact of dugong grazing. *Aquatic Botany*, *71*, 179–197. https://doi.org/10.1016/S0304-3770 (01)00181-4

- Mineur, F., Arenas, F., Assis, J., Davies, A. J., Engelen, A. H., Fernandes, F., Malta, E.-J., Thibaut, T., Van Nguyen, T. U., Vaz-Pinto, F., Vranken, S., Serrão, E. A., & De Clerck, O. (2015). European seaweeds under pressure: Consequences for communities and ecosystem functioning. *Journal of Sea Research*, *98*, 91–108. https://doi.org/10.1016/j. seares.2014.11.004
- Nakaoka, M., & Aioi, K. (1999). Growth of seagrass Halophila ovalis at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. Marine Ecology Progress Series, 184, 97–103. https:// doi.org/10.3354/meps184097
- Nakaoka, M., Mukai, H., & Chunhabundit, S. (2002). Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. *Ecological Research*, 17, 625–638. https://doi.org/10.1046/j.1440-1703.2002.00520.x
- Nordlund, L. M., Koch, E. W., Barbier, E. B., & Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS ONE*, 11, e0163091.
- Nowicki, R. J., Fourqurean, J. W., & Heithaus, M. R. (2018). The role of consumers in structuring seagrass communities: Direct and indirect mechanisms. In A. Larkum, G. Kendrick, & P. Ralph (Eds.), Seagrasses of Australia (pp. 491–540). Springer.
- Nowicki, R., Heithaus, M., Thomson, J., Burkholder, D., Gastrich, K., & Wirsing, A. (2019). Indirect legacy effects of an extreme climatic event on a marine megafaunal community. *Ecological Monographs*, e01365.
- Nowicki, R. J., Thomson, J. A., Burkholder, D. A., Fourqurean, J. W., & Heithaus, M. R. (2017). Predicting seagrass recovery times and their implications following an extreme climate event. *Marine Ecology Progress Series*, 567, 79–93.
- Nowicki, R. J., Thomson, J. A., Fourqurean, J. W., Wirsing, A. J., & Heithaus, M. R. (2021). Data from: Loss of predation risk from apex predators can exacerbate marine tropicalization caused by extreme climatic events. *Dryad Digital Repository*, https://doi.org/10.5061/ dryad.59zw3r261
- Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*, 1–12.
- Pearce, A. F., & Feng, M. (2013). The rise and fall of the "marine heat wave" off Western Australia during the summer of 2010/2011. *Journal of Marine Systems*, 111, 139–156.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214.
- Preen, A. (1995). Impacts of dugong foraging on seagrass habitats: Observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series*, 124, 201–213.
- Preen, A., & Marsh, H. (1995). Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland Australia. Wildlife Research, 22, 507–519.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982– 998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

RStudio Team. (2019). RStudio: Integrated development for R. RStudio Inc.

- Sheppard, J. K., Preen, A. R., Marsh, H., Lawler, I. R., Whiting, S. D., & Jones, R. E. (2006). Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. *Journal of Experimental Marine Biology* and Ecology, 334, 64–83. https://doi.org/10.1016/j.jembe.2006.01.011
- Smit, A. J., Brearley, A., Hyndes, G. A., Lavery, P. S., & Walker, D. I. (2005). Carbon and nitrogen stable isotope analysis of an Amphibolis griffithii seagrass bed. Estuarine, Coastal and Shelf Science, 65, 545–556. https://doi.org/10.1016/j.ecss.2005.07.002
- Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G. A., Burkholder, D., Fraser, M. W., & Zdunic, K. (2020). Too hot to handle: Unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Global Change Biology*, 26(6), 3525–3538. https://doi.org/10.1111/gcb.15065
- Thomson, J. A., Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Fraser, M. W., Statton, J., & Kendrick, G. A. (2015). Extreme temperatures, foundation species, and abrupt ecosystem change: An example from an iconic seagrass ecosystem. *Global Change Biology*, 21, 1463– 1474. https://doi.org/10.1111/gcb.12694
- Unsworth, R. K. F., Collier, C. J., Waycott, M., Mckenzie, L. J., & Cullen-Unsworth, L. C. (2015). A framework for the resilience of seagrass ecosystems. *Marine Pollution Bulletin*, 100, 34–46. https://doi. org/10.1016/j.marpolbul.2015.08.016
- Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E. et al (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140846.
- Walker, D. I. (1985). Correlations between salinity and growth of the seagrass Amphibolis antarctica (Labill.) Sonder & Aschers., in Shark Bay, Western Australia, using a new method for measuring production rate. Aquatic Botany, 23, 13–26.
- Walker, D. I., Kendrick, G. A., & McComb, A. J. (1988). The distribution of seagrass species in shark bay, Western Australia, with notes on their ecology. *Aquatic Botany*, 30, 305–317. https://doi. org/10.1016/0304-3770(88)90063-0
- Walker, D. I., Kendrick, G. A., & McComb, A. J. (2007). Decline and recovery of seagrass ecosystems—The dynamics of change. In A. Larkum, R. Orth, & C. Duarte (Eds.), Seagrasses: Biology, ecology and conservation (pp. 551–565). Springer.
- Waycott, M., Duarte, C. M., Carruthers, T. J., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck Jr, K. L., Randall

Hughes, A., Kendrick, G. A., Judson Kenworthy, W., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 12377–12381.

- Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., De Bettignies, T., Bennett, S., & Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*, 78.
- Wilmers, C. C., & Getz, W. M. (2005). Gray wolves as climate change buffers in Yellowstone. *PLoS Biology*, 3, e92.
- Wilmers, C. C., Post, E., Peterson, R. O., & Vucetich, J. A. (2006). Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters*, 9, 383–389.
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007a). Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Animal Behavior*, 74, 1085–1091.
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007b). Fear factor: Do dugongs (Dugong dugon) trade food for safety from tiger sharks (Galeocerdo cuvier)? Oecologia, 153, 1031–1040.
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007c). Living on the edge: Dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behavior*, 74, 93–101.
- Zarco-Perello, S., Wernberg, T., Langlois, T. J., & Vanderklift, M. A. (2017). Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, 7, 1–8.
- Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change. *Science*, *336*, 1516–1518.
- Zeileis, A., Cribari-Neto, F., & Grün, B. (2010). Beta regression in R. *Journal of Statistical Software*, 34, 1–24.

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